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INHERITANCE OF FECUNDITY IN THE DOMESTIC FOWL[1]

DR. RAYMOND PEARL

MAINE AGRICULTURAL EXPERIMENT STATION

THERE are under discussion at the present time two general views regarding certain fundamental points in heredity. Each of these points of view has its zealous adherents. On the one hand, is what may be designated the "statistical" concept of inheritance, and on the other hand, the concept of genotypes. By the "statistical" concept of inheritance is meant that point of view which assumes, either by direct assertion or by implication, that all variations are of equal hereditary significance and consequently may be treated *statistically* as a homogeneous mass, provided only that they conform to purely statistical canons of homogeneity. This assumption of equal hereditary significance for all variations is tacitly made in deducing the law of ancestral inheritance, when individuals are lumped together in a gross correlation table.[2] The genotype concept, on the other hand, takes as a fundamental postulate, firmly grounded on the basis of breeding experience, that two

[1] Papers from the Biological Laboratory of the Maine Experiment Station, No. 25. This paper was read at the meeting of the American Society of Naturalists at Ithaca, December, 1910.

[2] For a more detailed discussion of this point see a paper by the present writer entitled "Biometric Ideas and Methods in Biology: their Significance and Limitations," in the *Revista di Scienza* (in press).

sorts of variations can be distinguished, namely those (*a*) that are represented in the germinal material and are inherited without substantial modification, as in "pure lines," and those (*b*) that are somatic and are not inherited. By anything short of the actual breeding test it is quite impossible to tell whether a particular variation observed in the soma belongs to the one category or to the other. As I have tried to emphasize in other places, it is both to be expected on this view of inheritance, and is also the case in actual fact, that the somatic manifestation or condition of any character is a most uncertain and unreliable criterion of the behavior of that character in breeding. Finally under the genotype concept, of course, the whole array of facts brought out by Mendelian experiments find their place.

Now while certain adumbrations of the genotype concept have long been current in biological speculations in regard to heredity, this general view-point owes its grounding in solid facts primarily to Johannsen's work with beans and with barley. It is to be noted that in these cases, as well as in most of the investigations of the pure line theory which have followed Johannsen's work, the organisms used have been such as reproduced either by self-fertilization, or by fission, or by some vegetative process. This brings us to the consideration of a question of great importance, both theoretical and practical. In cases of dicœcious organisms, where a "*pure*" pedigree line in the sense that such lines are found in beans or in Paramecium by definition can not exist, has the genotype concept any bearing or significance? In a general way it obviously has. Probably no one (except possibly some of the ultra-statistical school) could be found who would deny that in general a distinction is to be made between variations having a gametic and those having merely a somatic basis. But specifically how far has the genotype concept any application in case of "non-selfed" organisms? Johannsen in his "Elemente" has thoroughly analyzed Galton's material and

shown that it is capable of a satisfactory and reasonable interpretation on the genotype hypothesis, and East and Shull have gone far in the analysis of genotypes in maize. This, however, is only a beginning. There is the greatest need for careful, thorough investigations of the inheritance of characters showing marked fluctuating variation in organisms having the sexes separate. Here lies one of the crucial fields in the study of inheritance to-day. Through the brilliant results in Mendelian directions and from the study of really "*pure*" lines we are getting clear-cut ideas as to the inheritance of qualitatively differentiated characters, such as color, pattern and the like, on the one hand, and in regard to the inheritance of quantitative variation in self-fertilized or non-sexually reproducing organisms, on the other hand. But beyond all these lie the difficult cases where in diœcious forms quantitative variations must be dealt with. If these can be cleared up and brought harmoniously into a general scheme or view-point regarding inheritance, we shall have gone a long way in the solution of this world-old biological problem.

For some four years past the writer has been engaged in a study of the inheritance of fecundity in the domestic fowl. The problem presented here is an important one from the practical as well as the theoretical standpoint. If definite and sure methods of improving the average egg production of poultry by breeding can be discovered it will mean much to the farmers of the nation. At the same time egg production is a character in some ways well adapted to furnish definite and crucial data regarding inheritance. Variations in egg production are readily measured, and can be directly expressed in figures.

The general results of this study of the inheritance of fecundity may be said, in a word, to be, so far as they go, in entire accord with the genotype concept, and not to agree at all with the "statistico-ancestral" theory of inheritance. Indeed, so ill is the accord here that the chief exponent of the latter doctrine has recently attempted to

throw the whole case out of court[3] by asserting that fecundity is not inherited in fowls, and that the present writer's investigations show essentially nothing more than that. It will be the purpose of this paper to present some figures sufficient to indicate with some degree of probability, I think, first that egg production in fowls *is* inherited, and second that it is probably inherited in accord with the genotype concept, in spite of the fact that we do not and can not here have "pure lines" in the strict sense of Johannsen's definition. In the present paper, owing to limitations of space, the whole of the data in hand obviously can not be presented. Only a few illustrative cases can be given here.

Before entering upon the discussion of the evidence it is necessary to call attention to two points. The first is in regard to the unit of measuring egg production used in the work. For reasons which have been discussed in detail elsewhere[4] the unit of study has been taken as the egg production of the bird before March 1 of her pullet year. This "winter production" is a better unit for the study of the inheritance of fecundity than any other which can be used practically. All records of production given in this paper are then to be understood as "winter" records, comprising all eggs laid up to March 1 of the first year of a bird's life. It may be said that the "normal" mean winter production of Barred Plymouth Rocks (the breed used in this work) is fairly indicated by the 8-year average of the Maine Station flock. This average November 1 to March 1 production is *36.12* eggs.[5] This figure is based on eight years continuous trap-nesting of the flock with which the present

[3] Pearson, K., "Darwinism, Biometry and some Recent Biology, I," *Biometrika*, Vol. 7, pp. 368–385, 1910.

[4] Bull. Me. Agr. Exp. Sta., No. 165. U. S. Dept. Agr. Bur. Anim. Ind., Bul. 110, Part II.

[5] It should be said that up to and including the winter of 1907 only the November 1 to March 1 records are available as a "winter" record. Since that time the small number of eggs laid before November 1 (on the average two or three per bird) are included in the "winter" totals. These, then, give, as stated, the total production up to March 1.

work was done, carried out before these investigations were begun.

In the second place it is desirable to call attention to some of the difficulties which attend an attempt to analyze the inheritance of the character egg production. The most important of these is the fact that this character is not visibly or somatically expressed in the male. A male bird may carry the genes of high fecundity, but the only way to tell whether or not this is so is to breed and rear daughters from him. All Mendelian workers will agree that it is sometimes difficult enough to unravel gametic complexities in the case of characters expressed somatically. It is vastly more difficult when only one sex visibly bears the character. In the second place a very considerable practical difficulty arises from the fact that egg production is influenced markedly by a whole series of environmental circumstances. The greatest of care is always necessary, if one is to get reliable results, to insure that all birds shall be kept under uniform and good conditions. Further, on this account, it is necessary to deal with relatively large numbers of birds. Some of the important conditions to be observed in work on fecundity have been discussed elsewhere[6] and need not be repeated here.

Turning now to the results we may consider first

The Effect of Selection for Fecundity in the General Population

On the "statistico-ancestral" view of inheritance it would be expected that if fecundity were inherited at all this character would respond to continued selection. That is, it would be expected, if the highest layers only were bred from in each generation, that the general flock average would steadily, if perhaps slowly, increase and that any level reached would be at least maintained by continued selection. In 1898 an experiment in selecting for high egg production was begun at the Maine sta-

[6] Me. Agr. Exp. Sta. Ann. Rept. for 1910, p. 100.

tion. In this experiment only such females were used as breeders as had laid over 150 eggs in their pullet year (corresponding roughly to an average winter production of 45 or more eggs) and the only males used were such as were out of birds laying 200 or more eggs in the year. This experiment was continued until the end of 1908. The selection, be it understood, was based on the egg record alone, and no account was kept of pedigrees or of genotypes. Every female with a record higher than 150 eggs in the year was used as a breeder regardless of whether her high fecundity was genotypic or phænotypic.

The results of this selection experiment covering a period of nine years have been fully reported elsewhere.[7] Here it needs only to be said that the net outcome of the experiment was to show that there was no *steady* or *fixed* improvement in average flock production after the long period of selection. There was no *permanently* cumulative effect of the eight (in the last year) generations of selected ancestry. So far from there having been an increase there was actually a decline in mean egg production concurrent with the selection, taking the period as a whole. During parts of the selection period, however, as for example the years 1899–1900 to 1901–02, inclusive, and the years 1902–03 to 1905–06, inclusive, an improvement from year to year was to be noted, but in each case the flock dropped back in intervening years. This is an important point, the meaning of which is now clear. The flock average from year to year depended largely upon *whether the breeders of the year before had had their high fecundity genetically represented or only somatically.* In some years the selection was fortunate in getting nearly all the breeders from good (*i. e.*, "high production") genotypes or from good *combinations* of genes. In other years just the opposite thing happened: the high layers chosen as breeders came from low geno-

[7] U. S. Dept. Agr. Bur. Anim. Ind., Bul. 110, Parts I and II, 1909 and 1911. *Zeitschr. f. indukt. Abst. a. Vererb.-Lehre,* Bd. 2, 1909, pp. 257–275.

types or combinations of genes. The general upshot was that while the selection of *high layers* merely as such was systematic year after year the result attained in the general flock production was entirely haphazard and uncertain. This is exactly what would be expected on the genotype hypothesis, but not on the "statistico-ancestral."

TABLE I

MEAN WINTER (NOVEMBER 1 TO MARCH 1) EGG PRODUCTION DURING THE SELECTION EXPERIMENT

Year	Mean Winter Production
1899–1900	41.03
1900–01	37.88
1901–02	45.23
1902–03	26.01
1903–04	26.55
1904–05	35.04
1905–06	40.66
1906–07	21.44
1907–08	15.92

The actual course of the average winter egg production (not hitherto published) during the period is given by the figures of Table I and shown graphically in Fig. 1.

Certainly the first line of evidence, derived from a long-continued experiment, involving more than 2,000 individuals, gives no support to the "statistico-ances-

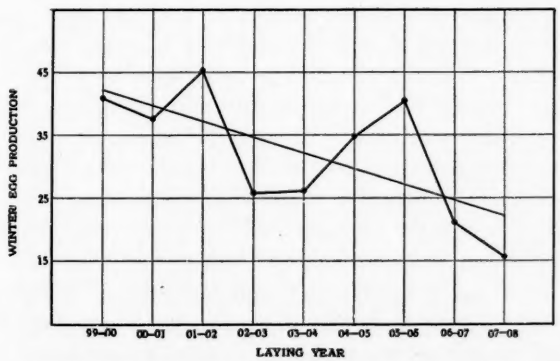


FIG. 1. Diagram showing the course of average winter egg production during the period covered by the mass selection experiment.

tral'' theory and indeed is in flat contradiction to one of the most fundamental tenets of that faith.

Let us next consider the question,

ARE SOMATICALLY EQUAL VARIATIONS IN FECUNDITY OF EQUAL HEREDITARY SIGNIFICANCE?

In the spring and summer of 1907 were reared 250 pullets, all of which were the daughters of hens that had laid approximately 200 or more eggs in the first year of their life. This group of mothers was reasonably homogeneous in respect to records of egg production. All had laid about the same number of eggs. Their daughters were, however, far from a homogeneous lot with respect to egg production.[8] It is plain from the results obtained in that experiment that the egg record of a hen is a most unreliable criterion of the probable number of eggs which her daughters will lay. This is demonstrated by examination of individual cases. Thus consider the two mothers nos. 253 and 14. Their winter production records were nearly identical (65 and 66 eggs, respectively). Their daughters' average winter productions were 23.87 and 2.40 eggs, respectively! Certainly it seems reasonable to conclude that the gametic constitutions involved in the breeding of 253 and 14 were quite different, though both these hens laid the same number of eggs. Again, take birds no. 386 and 911. One had a winter record of 55 and the other of 52 eggs. Yet their daughters' average winter productions were, respectively, 4.88 and 27.33 eggs. Many more instances of this kind could be brought forward. Taken together, the whole evidence shows beyond the shadow of a doubt that the presence of high fecundity in an individual, and that factor which makes high fecundity appear in the progeny, are two very different things, either of which may be present in an individual without the other. We plainly have here the basis for the distinction of phænotypes and genotypes just as in beans.

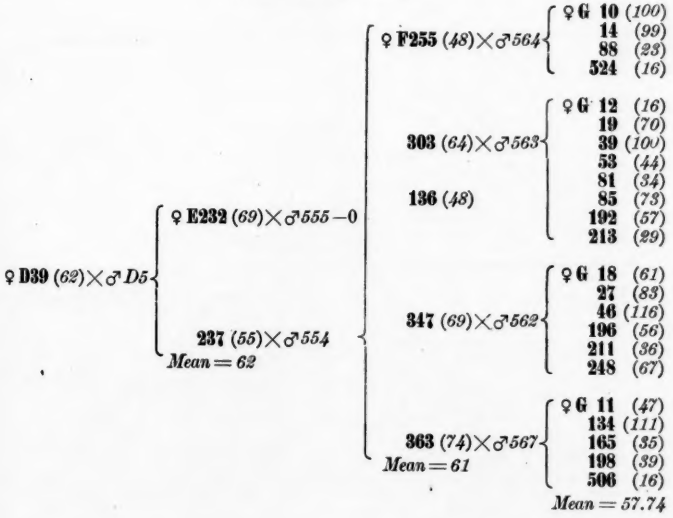
[8] Full details regarding this experiment have been published as Bull. 166, Me. Agr. Exp. Sta., 1909. See particularly Table I.

The Inheritance of Egg Production in Pedigree Lines

Let us now consider some of the evidence that such things as genotypes of fecundity really exist in fowls. We may first examine some representative pedigrees covering four generations and showing the occurrence of high and low fecundity lines.

As a typical example of a high fecundity pedigree line in which the high fecundity is genotypic, line D5D39 may be considered. In the presentation of this and other pedigree tables the following conventions are adopted. The band numbers of the birds are in bold-faced type, and following the band number of each female, her winter egg record is given in italic figures enclosed in parenthesis. The band numbers of males are given in italics.

Pedigree Line D5D39



This line is shown graphically in Fig. 2.

Little comment on this pedigree line is necessary. We see a certain high degree of fecundity faithfully reproduced generation after generation. Different males were

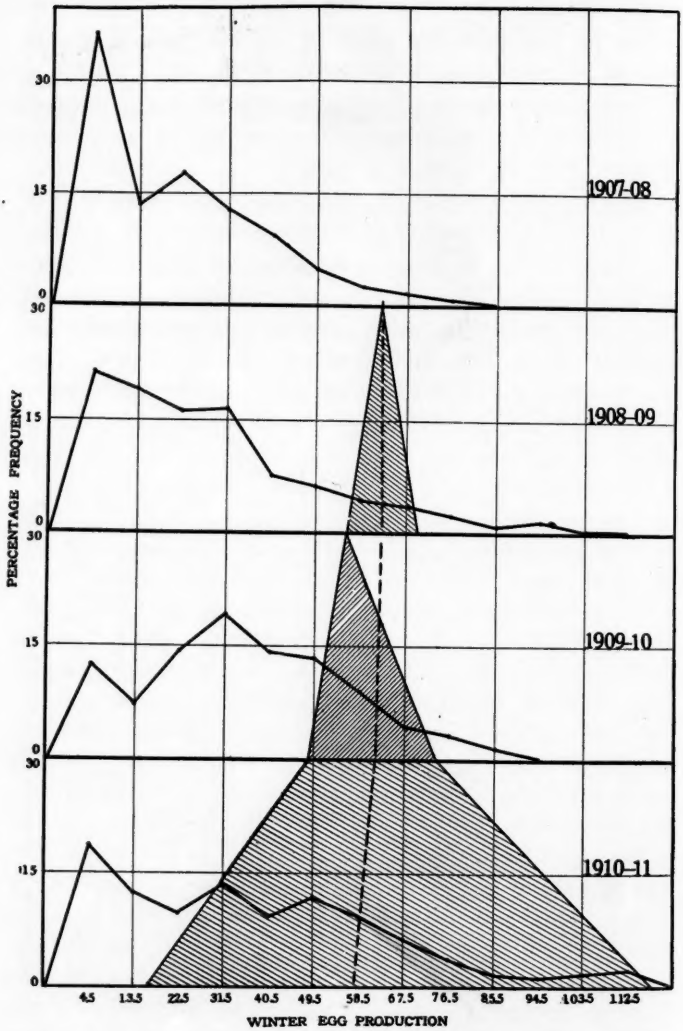


FIG. 2. Diagram showing range of variation and mean fecundity in each generation of line D5D39. The main polygons of variation give the distribution of fecundity in the general flock in each generation. The cross-hatched areas represent the pedigree line, and the heavy dotted lines through these areas represent the mean fecundity of the line in each generation.

used with different females, but in every case the males used were from high fecundity lines and were believed to carry this quality in their germ cells either in homozygote or heterozygote condition.

In marked contrast to the last example let us consider the *low* fecundity line D61D168. It is a troublesome matter to propagate the low fecundity lines, because of the difficulty of getting a sufficient number of eggs during the early part of the breeding season. The line D61D168 is of interest not alone as an illustration of a typical low line, but also because there appeared in it a mutation, or something very like one. We will consider here only the main line and not the mutant.

PEDIGREE LINE D61D168

♀ **D168**(*33*)×♂ *D61*

- ♀ **E231**(*25*)×♂ *552*
- **419** (*9*)×♂ *551*
- **209**(*38*)×♂ *555*—0
- **313**(*26*)×♂ *554*
- **363**(*11*)×♂ *550*
- **15**(*18*)
- **163** (*9*)
- **200**(*12*)
- **141** (*0*)
- **116**(*28*)
- **151**(*11*)
- **24**(*23*)
- *Mean=17.5*
- ♀ **E248**(*48*)[9]

♀ **F233**(*32*)×♂ *573*—0

♀ **F165** (*7*)×♂ *569*

- ♀ **6221**(*16*)
- **430**(*12*)
- **477** (*1*)
- *Mean=9.67*

- ♀ **F250**(*20*)
- **174**(*21*)
- ♀ **F249**(*30*)
- *Mean=22*

This line is shown graphically in Fig. 4, in which the mutant and its progeny are also shown.

A low line in which no mutant has appeared, but in which also the mean production is not so low as in line D61D168 is D65D366. Since the egg production has not been so low in the early part of the breeding season with this line it has been easier to propagate it.

[9] This was the mutant referred to. Its progeny will be considered later. See p. 335.

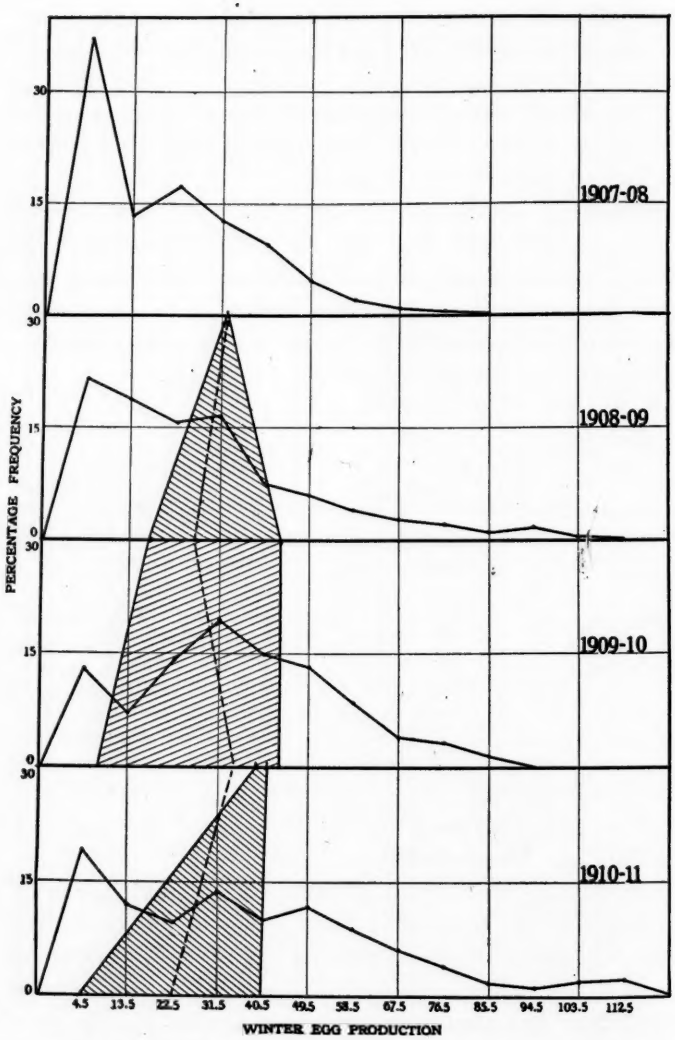


FIG. 3. Diagram showing range of variation and mean fecundity in each generation of line D65D366. Significance of lines and cross hatching as in Fig. 2, *q.v.*

PEDIGREE LINE D65D366

♀ D366(33) × ♂ D65

- ♀ E239(24) × ♂ 553
  - ♀ F309 (OD)[10]
  - 263(44)
  - 362(43)
  - 216(41) × ♂ 569
    - ♀ G 34 (4)
    - 42 (37)
    - 56 (40)
    - 164 (5)
- 224(43) × ♂ 554
  - ♀ F301 (7)
  - 223(14)
  - 224(42)
- 354(15) × ♂ 551
  - ♀ F242(21)
  - 221(39) × ♂ 566
    - ♀ G 65 (28)
    - 209 (33)
    - 267 (25)
    - 502 (21)
    - 544 (8)
- 331(31) × ♂ 552—0
- 344(17)
  - × ♂ 550
  - × ♂ 528
  - ♀ F271(37)
  - ♀ F171(46)

Mean=26 *Mean=33.4* *Mean=22.33*

This line is shown graphically in Fig. 3.

In the examples thus far given we have had to do with pedigree lines in which a given degree of fecundity reappeared from generation to generation with practically no change. In two instances quite certainly, and possibly in several others, a new and distinct variation has suddenly appeared within a line and thereafter bred true, thus presenting the characteristic phenomena of mutation. The most striking instance of this sort occurred in line D61D168 and may be given here in detail. The main part of this line has already been discussed (p. 331). It will be recalled that it is a line of low fecundity. In 1908 there appeared in it one individual of distinctly higher fecundity than any other bird in the large family of that year. This individual when bred produced only high layers. In the next generation two of these daughters were bred to males known to belong to high fecundity genotypes (♂♂ 554 and 566). One of these matings unfortunately produced no adult female offspring. The other led to the production of six adult daughters, all of which are relatively high layers, with the single exception of G495, which has a record of only one egg, and that record is doubtful. This bird has probably never laid an egg, and almost certainly is pathological.

[10] Bird died during winter period.

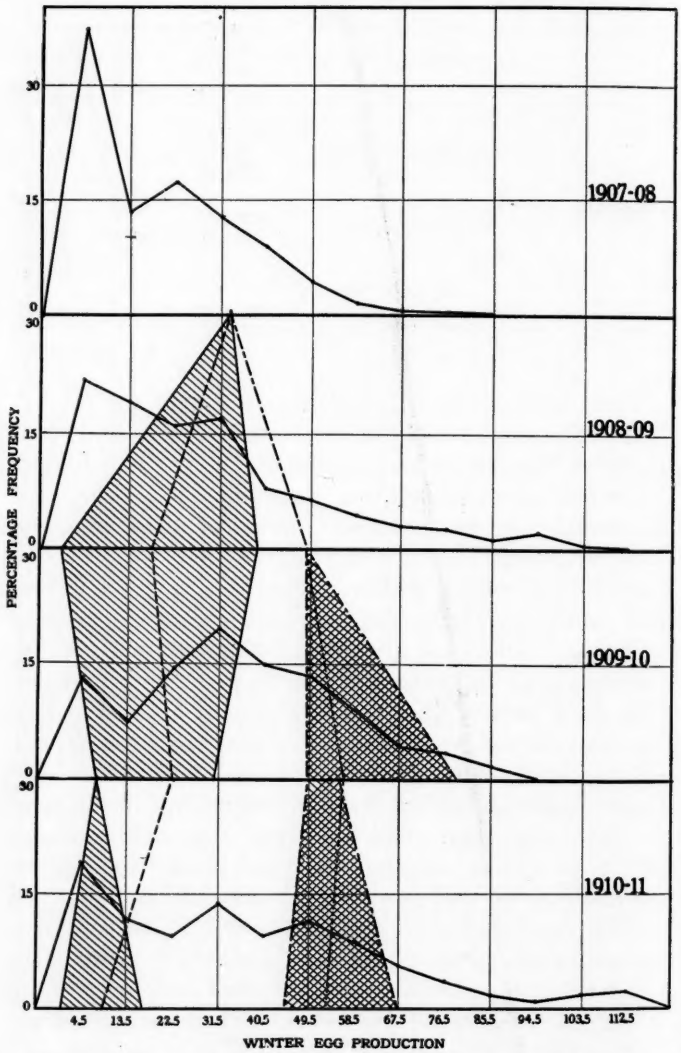


FIG. 4. Diagram of pedigree line D61D168. The significance of lines is the same as in Figs. 2 and 3, except that the mutant line is double cross hatched. For the sake of simplicity E495 and the daughters of D31 are omitted in the 1910–11 generation.

Leaving this bird out of account because pathological, the mean winter production of the family is 52.8 eggs, very strikingly different from the average (9.67 eggs) of the birds of the same generation in the main low line in which the mutation appeared.

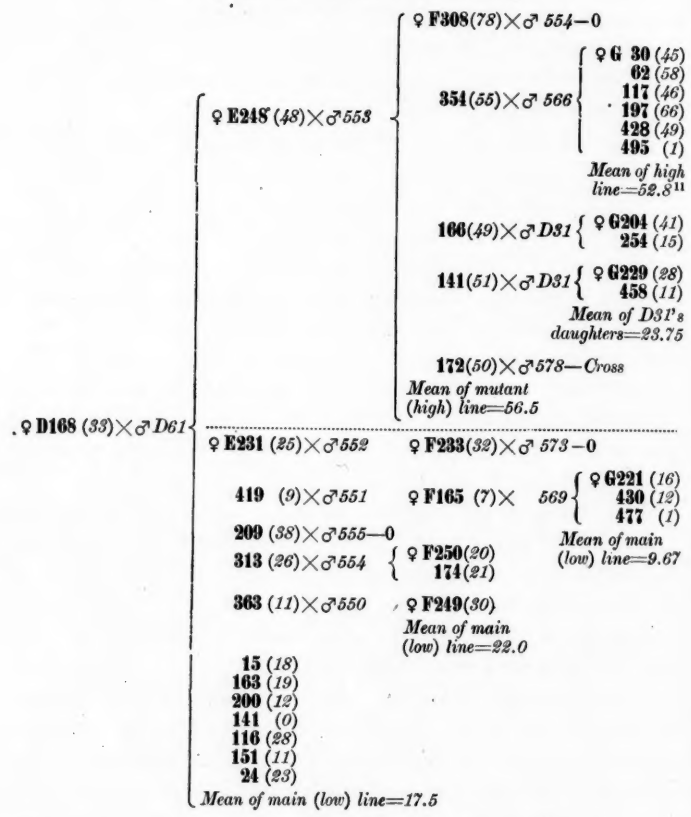
Two other daughters of the mutant E248 were mated to ♂D31, a bird known not only to belong to a genotype of mediocre to low fecundity, but to be remarkably prepotent in respect to this character, so that practically regardless of the females with which he has been mated the get has been uniformly poor in respect to egg production. Four adult females resulted from the two matings under discussion. They have an average winter production of 23.75 eggs. There are several possible explanations of this result, but the most probable is that we have here simply one more instance of the extraordinary prepotency of ♂D31.

The last of the daughters of the mutant was mated to a cross-bred male, no. 578, and consequently the progeny can not fairly be compared with the pure Barred Rocks in respect to fecundity.

The facts here briefly discussed are shown in the following table and graphically in Fig. 4.

It is apparent from the table and the diagram that the main line and the "mutant" line are entirely distinct. Indeed they do not overlap in their ranges even excepting only the pathological individual G495. The "mutant" pullet E248, for some reason or other, possessed the capacity both to lay a relatively large number of eggs, and the genes necessary to make this quality appear in her progeny. Whether this individual is to be regarded as a true "mutation" would appear to be largely a question of definition. In the writer's opinion the most probable explanation is that E248 is a Mendelian segregation product. That is, let it be supposed that both D168 and D61 were heterozygous with respect to degree of fecundity, and were producing in some (unknown) ratio both "high fecundity" and "low fecun-

PEDIGREE LINE D61D168 (COMPLETE)



dity'' gametes. Then E248 may be supposed to have originated from the union either of two ''high fecundity'' gametes or one high and one low fecundity gamete. She then would be either a DD or a DR bird, on the assumption, which the facts seem to support, and which I have more fully discussed elsewhere,[12] that high fecundity is dominant over low.

[11] Omitting G495. See text.

[12] ''Inheritance in 'Blood Lines' in Breeding Animals for Performance, with Special Reference to the '200-egg' Hen,'' Rept. Amer. Breeders' Assoc., Vol. VI, 1911 (in press).

The subsequent breeding history of E248 indicates that it was probably a DD bird, though the reasons for this opinion can not be fully gone into here. The general view, recently emphasized by Nilsson-Ehle,[13] that phenomena of mutation are, in many cases at least, merely cases of Mendelian segregation has much evidence in its favor.

The pedigrees which have been given are merely illustrations. Many other similar ones might be cited from the records in hand did space permit. In the experiments during the past three years the attempt has been made to propagate separately lines of high, medium and low fecundity. In the course of this work it has been found that lines of high fecundity were nearly if not quite as likely to have originated with individuals of a low record of production as with those of a high record. Similarly, many low fecundity lines have originated with individuals which were themselves exceedingly high layers. Indeed one of the highest winter layers which have ever appeared in the stock evidently belonged to a genotype of very low fecundity, since it has never been able to produce progeny of anything but the poorest laying capacity. The breeding history of this bird (D352) is indeed so interesting that it may be briefly discussed here. This bird in her pullet year laid 98 eggs between November 10 and March 1 and made a record for the year of over 200 eggs. She was mated and produced plenty of eggs during the hatching season, but they hatched very badly. Only one female worth putting in the house was obtained. This pullet (E356) made a winter record of only 39 eggs, just about the general flock average. E356 was not mated. Her mother (D352) was kept over and bred to another male the next year, in the hope that as a fowl she might produce more and better chickens than she had as a pullet. As a matter of fact she was again able to produce during the whole

[13] Nilsson-Ehle, H., "Kreuzungsuntersuchungen an Hafer und Weizen," *Lunds Univ. Arsskr.*, N. F., Afd. 2, Bd. 5, Nr. 2, 1909, pp. 1–122.

breeding season only one pullet worth putting into the laying house. This pullet (F163) made a winter record of but 11 eggs. F163 was bred in 1910, but produced only one daughter worth saving. This daughter, G429, has made a winter record of 18 eggs. It would be hard to get clearer evidence than that afforded by this breeding history that D352 belonged to a low fecundity genotype, in spite of her individual high laying record.

THE EFFECT OF THE SELECTION OF FECUNDITY GENOTYPES

Let us now consider the bearing of the results so far set forth on the problem of selection. Taking first the question of the effect of selection for fecundity within a population it is plain that if different degrees of fecundity have a genotypic basis, as the facts above presented and a considerable mass of data of a similar kind, which owing to lack of space can not be given here would appear to indicate, then the results following selection will depend entirely upon the genotypic constitution of the population. If high fecundity genotypes are present they can be isolated by selection. If they are not present selection of high laying hens will not change the average production of the flock.

The aim of the selection experiments since 1907 has been to discover and propagate separately genotypes of high fecundity and genotypes of low fecundity, all the birds being taken from the same general flock. The results of this work are shown in the following table and in Fig. 5. This table is to be regarded as a continuation of that given on p. 327, *supra,* which shows the results of mass selection for high fecundity in the same stock.

EFFECT OF SELECTION FOR FECUNDITY WITHIN THE POPULATION

1907–08.	Mean winter production of general population	15.92
1908–09.	Mean winter production of all high fecundity lines	54.16
1908–09.	Mean winter production of all low fecundity lines	22.06
1909–10.	Mean winter production of all high fecundity lines	47.57
1909–10.	Mean winter production of all low fecundity lines	25.05
1910–11.	Mean winter production of all high fecundity lines	50.58
1910–11.	Mean winter production of all low fecundity lines	17.00

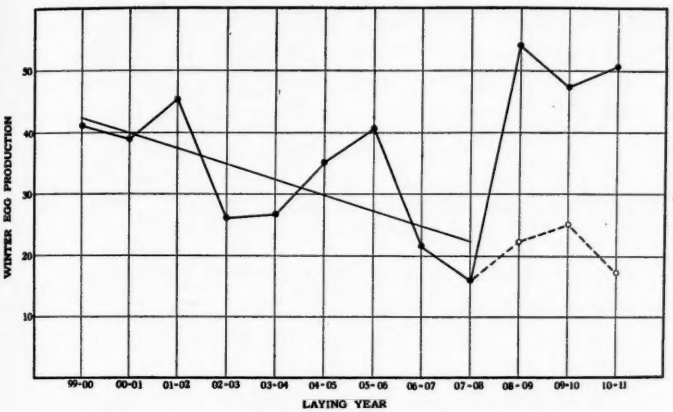


FIG. 5. Showing the effect of selecting high and low fecundity on a genotypic basis. The solid line denotes means of all "high lines"; the dotted line means of all "low lines." Up to 1907–08 the attempt had been to increase egg production by breeding merely from the highest layers, regardless of pedigrees. In 1907 and subsequent years the attempt has been to isolate genotypes of high and low fecundity which shall breed true, each to its own type.

The results indicate the effectiveness of this method of selection. It should be understood, of course, that only those pedigree lines are included in the high line averages which uniformly *in each generation* show high fecundity. A similar consideration applies to the low line averages.

Let us now consider briefly the question of the effectiveness of selection *within* the genotype. According to the "pure line" concept we should not expect selection of high or low individuals belonging to the same genotype to produce any effect, except in cases where segregation has occurred and the selected individuals are really gametically different, though having the same pedigree. An example of this sort has been given in the case of line D61D168 (cf. p. 331, *supra*). The ineffectiveness of selection within the line when something of this sort does not occur is illustrated by line D56D407. In the F_1 generation in this line there were four birds, of which three were good layers and one was a poor layer. Two of the good layers and the poor layer were bred.

Large families were reared in F_2 and F_3. The average results in the three generations are given in the following table.

EFFECT OF SELECTION OF GOOD AND POOR WINTER LAYERS IN THE SAME LINE, D56D407

Generation	F_1	F_2	F_3
Mean winter record of *good* layers and their progeny	76.0	46.7	35.57
Mean winter record of *poor* layers and their progeny	26.0	52.0	36.75[14]

It is evident that selection within the line here was quite without effect.

Another example of the same thing from line D31D447 may be given by way of further illustration. In this line there was in the F_1 generation a family of ten daughters. Of these some were very good and some were poor layers. All were bred. The mean results are shown in the next table.

EFFECT OF SELECTION OF GOOD AND POOR WINTER LAYERS IN THE SAME LINE, D31D447

Generation	F_1	F_2	F_3
Mean winter record of *good* layers and their progeny	62.5	23.75	22.00
Mean winter record of *poor* layers and their progeny	32.0	28.75	14.75

Here again it is plain that selection within the line was without effect. Many more examples of the same sort might be given from the records did space permit. In general there is no evidence whatever that the selection of individuals of different laying records, but belonging to the same fecundity genotype, produces any definite or permanent effect whatever.

DISCUSSION AND CONCLUSIONS

Taking into consideration all the facts which have come out of this study, one is led to the following view as to the composition of a flock of fowls in respect to fecundity. In the average flock we may presume that there will probably be represented a number of fecundity

[14] If one family of four birds, which ought not in fairness to be included here because they were extremely inbred (brother-sister mating) in connection with another experiment, is excluded this average becomes 49.0.

genotypes, some high, some low, and some intermediate or mediocre. In an ordinary flock these genotypes will be greatly mixed and intermingled. Further, the facts in hand indicate that the range of variation in fecundity *within* the genotype is relatively very large, nearly as great, in fact, as in the general population. Thus while fecundity genotype *means* may be and usually are perfectly distinct, there is much overlapping of individuals in the different lines. In consequence it results that the egg record of an individual bird is of almost no value in helping to tell in advance of the breeding test to what fecundity genotype it belongs. Essentially this same fact has been brought out in all of the work which has been done with pure lines. The only difference in the present case lies in the fact that the range and degree of variation within the line appears to be relatively greater in the case of fecundity than in the case of most characters hitherto studied, as, for example, size relations in beans or *Paramecium*.

The most serious difficulty which confronts one in the attempt to analyze the inheritance of a character like fecundity lies in the almost inextricable mingling of genotypes in the great majority of individuals. This, of course, is a direct consequence of the manner of reproduction. The germ plasm of two separate individuals must unite to form a new individual. By prolonging incestuous mating one may in theory come indefinitely close to reproductive purity, but in practise even this is extremely difficult, if not impossible of accomplishment on any large scale or through any long period of time. The fact simply is that a "pure line" in the strict sense of Johannsen[15] can not by definition exist in an organism reproducing as the domestic fowl does. This, however, by no means indicates that the inheritance of fecundity does not rest on a genotype basis, or, in other words, that

[15] Johannsen's definition is as follows: "Mit einer reinen Linie bezeichne ich Individuen, welche von einen einzelnen selbstbefruchtenden Individuum abstammen." ("Ueber Erblichkeit in Populationen und reinen Linien," p. 9.)

fowls do not carry definite genes for definite degrees of fecundity.

We touch here upon an important point; namely, the relation of the mode of reproduction to the mode of inheritance. As one reflects upon the matter it becomes clear that it is only in the sense of a *reproductive* line that we can not, by definition, have pure lines in organisms where the sexes are separate. It is perfectly possible to have a line of such organisms in which all the individuals are *gametically* pure with reference to any particular character. For example, it is the simplest of matters to establish a line of horses pure in respect to chestnut coat color. Any individual in such a line mated to any other will never produce anything but chestnut offspring. So similarly with any other character, it is only necessary to obtain homozygous individuals in respect to any character in order to form a gametically pure strain with reference to that character.

It must further be kept clearly in mind that a reproductive "pure line" (in the sense of Johannsen's definition) may be made up of individuals *not* gametically pure (*i. e.*, homozygous). Thus suppose one crosses a yellow and a green pea and then takes an F_2 heterozygote individual seed which originated from a self-fertilized F_1 individual as the "single, self-fertilized individual" with which to start a line. The individual which starts such a line arose by self-fertilization and is selfed to produce progeny and would thus fulfil every requirement of a *reproductive* "pure line" as defined by Johannsen. Yet it would produce both yellow and green offspring. On the other hand, as already pointed out, a line which is not, and from the nature of its mode of reproduction never can be, reproductively "pure" may be gametically so (*i. e.*, have none but homozygous individuals with respect to any character).

We then see that the fact that in fowls the sexes are separate and we therefore can not have reproductive "pure lines" gives, *per se*, no reason to suppose that fe-

cundity is not inherited on a genotypic basis. We have to consider the problem of genetic or gametic purity. Do we have homozygote lines in such cases as those discussed in this paper? It plainly is the fact that one can get lines of birds which, broadly speaking, will breed true (perhaps throwing occasionally a few individuals not true to the type of the line) to definite degrees of fecundity. The same thing is true of milk production in dairy cattle, speed in race horses, etc. What are these lines gametically? Theoretically the formation of gametically pure (homozygote) lines with respect to definite degrees of fecundity is simple. Practically it is exceedingly difficult to do this, owing to the fact that (*a*) the character studied is not expressed in the male, and (*b*) it is subject to a wide fluctuating variability caused by environmental conditions. The question as to the gametic constitution of the fecundity lines here discussed obviously can not be answered finally now. It is a matter for much further research. One may, however, form a general conception of the probable gametic constitution of such lines, which has much evidence in its support. The essential points in such a conception are:

1. Probably no line yet obtained is absolutely pure gametically in respect to fecundity. It represents a mixture of a greater or less number of fecundity genes.

2. Lines which breed reasonably true to a definite degree of fecundity may in most cases be taken to be made up of individuals bearing a preponderant number of genes of the particular degree of fecundity to which the line breeds true, so that in gametogenesis a great majority of the gametes formed carry only these genes. They also carry some genes of higher, or lower fecundity, or both kinds. When individuals of a definite (*e. g.*, "high") line thus constituted are bred together the majority of the offspring will, purely as a matter of chance, be produced by the union of two high fecundity gametes. It is quite possible that with families of the size obtained with poultry nearly or quite every individual produced

in the line for several successive generations may be of this kind. In the long run, however, it is to be expected that a small number of "off" individuals will appear in the line. These originate by the chance union of two low fecundity genes, or by the union of a "high" gene with a "low" gene of great potency (as in the case of D31, cf. p. 335).

3. The degree to which such a line will breed true will depend upon the proportion of genes of one type (or of very similar types) present. The higher such proportion the less frequently will the "off" individual segregate out. The practical goal to be worked towards is, of course, to obtain several lines not closely related, but all made up only of individuals homozygous with respect to either high or low or any other definite degree of fecundity.

Whether a given degree of fecundity is to be regarded as a single unit character, in the Mendelian sense, or, on the other hand, as a complex dependent upon a particular combination of separately segregable unit characters, can not yet be determined. Every one must recognize the fundamental importance of the investigations of Nilsson-Ehle, Baur and East, which have shown that many characters which at first glance do not appear to conform to any determinate law of inheritance are really complexes, formed by the combination of a number of unit characters, each of which segregates and otherwise behaves in a perfectly regular and lawful manner. There are some facts which indicate that high fecundity is a character of this kind, but it will require prolonged analysis to decide this, because of the numerous practical difficulties which attend the study of fecundity.

A great help in this analysis, as well as a contributory line of evidence of much weight in supporting the general conception of the manner of inheritance of fecundity set forth above, is derived from the study of crosses between breeds of poultry in which high and low degrees of fecundity are definite breed characters. Studies of

this sort carried out at the Maine station indicate that the relatively high fecundity characteristic of the Barred Rock breed is inherited as a sex-limited character. In this respect it behaves like a simple unit character, but this does not necessarily prove that it is not a complex. More data are needed to settle this point. Of much significance is the fact that, whether simple or complex, fecundity is shown by these experiments in cross breeding to be a character resting on a definite gametic basis.

In conclusion, I think it may fairly be said that the investigations here reported show in the first place that different degrees of fecundity *are* inherited in the domestic fowl, and in the second place, that in all respects wherein it has been possible, considering the inherent difficulties of the material and the character dealt with, to make the test, the method of this inheritance is in entire accord with Johannsen's concept of genotypes.

THE BIOMETRIC PROOF OF THE PURE LINE THEORY[1]

DR. J. ARTHUR HARRIS

CARNEGIE INSTITUTION OF WASHINGTON

I. INTRODUCTION

ON this platform I find myself in a somewhat embarrassing position. A friend assured me in advance that this symposium would be somewhat analogous to the country parson's "praise service," and into this pure devotional atmosphere I must bring a note of agnosticism.

Agnosticism is a term selected after careful deliberation. Johannsen's propositions are important—if true—and any candid naturalist must hesitate before opposing a new theory which may lead to important advances in biology. Agnosticism is the condition of mind temporarily enforced by the results of my own experiments. If one is pledged in advance to the pure line theory many of these observations can be made to confirm Johannsen's conclusions. If one is unprejudiced and seeks to fit his theories to his observations, rather than to adjust his facts to his preconceived conclusions, the results are quite as capable of other interpretation. Possibly more extensive work may show clear confirmation of his results. Meanwhile I must withhold final judgment, merely stating that my own work has greatly shaken my confidence in Johannsen's theory.

Here I do not care to dwell upon details of my own experiments. It seems more profitable to try and state the fundamental problems of the pure line theory as they appear to the biometrician and to indicate the methods of work which seem to him necessary to the drawing of sound conclusions.

[1] From a symposium on "The Study of Pure Lines of Genotypes," before the American Society of Naturalists, December 29, 1910.

II. The Fundamental Propositions of the Pure Line Theory

Our symposium has for its subject the Genotype or Pure Line Theory. Some of the speakers have enthusiastically urged us to replace the words "pure line theory" by "pure line facts." If this were done there would be little need for this program. Pure line facts are as yet a very insignificant part of biological data. The real occasion for this symposium is the pure line theory—the rank vines which have grown from the nineteen bean seeds which Johannsen planted in 1901. Biologists would have been little interested by the statement that selection within the offspring of a single bean has been ineffective in changing the weight of the seed. It is the daring generalization of the conclusions drawn from these limited experiments—the curt characterization of other researches as of no biological significance or their reinterpretation (from flounder's fins to intelligence in school children) in terms of the bean experiments, that forces us to take an interest in these matters.

Our first problem is to ascertain what these generalizations—the elements of the pure line theory as contrasted with the pure line facts—are. Our second task is to try to ascertain in how far experimental facts support the pure line theory.

Davenport[2] has given a particularly good outline of Johannsen's theory:

> The fundamental principle of Johannsen is that an ordinary frequency polygon is usually made up of measurements of a characteristic belonging to a non-homogenous mass of individuals; that it is really analyzable into several elementary masses each of which has a "frequency polygon" of its own. In each elementary polygon the variation is strictly due to non-inheritable somatic modifications, selection of extremes of which has no genetic significance. But the selection for breeding of individuals belonging to different elementary polygons, lying, say, at the extremes of the complex, may quickly lead to an isolation of these elementary polygons, the constituent individuals of which reproduce their peculiarities as distinct elementary species.

[2] Davenport, C. B., *Science*, n. s., 30: 852, 1909.

We recognize three essential propositions:

Proposition 1.—Most species or varieties are not homogeneous, but are composed of a large number of minor forms.

The series of individuals classified as the same variety or race by the systematist, regarded as homogeneous material for experiment by the physiologist, lumped together to form a single "population" by the statistician, is designated by Johannsen as a phænotype. This phænotype may generally be analyzed by pure line breeding into many constant and indivisible strains known as genotypes.

Systematists have long regarded certain groups as polymorphic. *Aster, Rubus, Salix* and *Cratægus* at once occur to the botanist and *Unio, Salmo* and the staphylinids to the zoologist. But the genotype theory seems to regard systematic polymorphism as a much wider phenomenon. Indeed one is sometimes assured that every apparently uniform cultivated variety is a swarm of constant biotypes. Johannsen emphasizes the generality of heterogeneity. For instance, he says:[3]

> Ein gegebener Phaenotypus mag Ausdruck einer biologischen Einheit sein; es braucht es aber durchaus nicht zu sein. Die in der Natur durch variationsstatistische Untersuchungen gefundenden Phaenotypen sind es wohl in den allemeisten Fällen nicht![4]

Again on page 162:

> In der Praxis wirkt ein Selektion meistens schnell in der beabsichtigen Richtung—eben weil die Bestände oder Populationen fast immer Gemische sind.

One more illustration will suffice:

> Der oft ausserordentlich grosse Reichtum genotypischer Unterschiede in einer auscheinend einheitlichen Population war von Darwin . . . ebensowenig in der vollen Tragweite erkannt, als es dem grossen Grundleger der Mikrobiologie, Pasteur, klar sein konnte, welche bedeutung es hatte,

[3] "Elemente," p. 123.

[4] On page 121, he remarks on this point: "Selbst die shönste 'typische' Verteilung beweist gar nichts in Bezug auf Einheitlichkeit des derart in Erscheinung tretenden Typus." Professor Johannsen is apparently unaware that this point has been fully recognized by "Biometriker" for years.

dass viele physiologisch sehr differierende Heferassen in vermeintlich 'reinen' Hefekulturen koexistieren konnten.[5]

Proposition 2.—These genotypes are separated generally by differences which are exceedingly minute.

Notwithstanding the constant flood of new species segregated from the classic Linnean groups, necessitating frequent supplements to "Index Kewensis" and other works of its kind, many naturalists could hardly understand the small species discussed by de Vries in his great work. Indeed, many laboratory men hardly perceived the usefulness of recognizing species—perfectly constant, we were assured—so closely related that one taxonomist could not identify the species of another from his descriptions; species so similar that herbarium material was worthless, and only culture side by side could distinguish them. Yet after a lapse of only ten years we find de Vries criticized for not recognizing even smaller divisions than these! Spillman says: "de Vries overlooks entirely those closely related pure lines, differing frequently only quantitatively, and in a single character. . . . They not only do not differ in all their characters as the *Œnothera* mutants do, but their norms present a regular series coming under Quetelet's law."[6]

As examples of these minute differences both he and Lang[7] quote the "72 Formen einer Population einer gewissen Heferasse" discussed by Nilsson-Ehle.[8]

Jennings says:[9]

> The work with genotypes brings out as never before the minuteness of the hereditary differences that separate the various lines. These differences are the smallest that can possibly be detected by refined measurements taken in connection with statistical treatment. Johannsen found his genotypes of beans differing constantly merely by weights of two or three hundredths of a gram in the average weight of the seed. Genotypes of *Paramecium* I found to show constant hereditary differences of one two-hundredths of a millimeter in length. Hanel

[5] "Elemente," p. 318.
[6] Spillman, W. J., AM. NAT., 44: 760, 1910.
[7] Lang, A., *Arch. f. Induktive Abstamm.- u. Vererlungsl.*, 4: 15–16, 1910.
[8] Nilsson-Ehle, H., *Bot. Not.*, 1907: 113–140.
[9] Jennings, H., AMER. NAT., 44: 144–145, 1910.

found the genotypes of *Hydra* to differ in the average number of tentacles merely by the fraction of a tentacle. That even smaller hereditary differences are not described is certainly due only to the impossibility of more accurate measurements; the observed differences go straight down to the limits set by the probable errors of our measures.

Proposition 3.—These genotypes are rigid hereditary units; by a process of mutation one may give rise to another, but selection within the genotype is incapable of effecting a change.

This theory is everywhere so prominent in the writings of the genotypists that discussion or explanation is superfluous.

III. The Cardinal Proposition of the Genotype Theory

Of these three essential propositions of the genotype theory of heredity, the first two might be accepted by Darwinian or Lamarckian or by a member of almost any school. If the proposition concerning the exceeding smallness of the differences be true, the theory might seem to present the greatest difficulty to the de Vriesian,[10] for with smaller and smaller genotypes there is a constant approach to continuity, but we are assured that continuity is never realized.[11]

The third proposition—that genotypic differences are rigid and unchangeable except by mutation—is therefore the essential one. The most obvious way in which this hypothesis can be tested against concrete facts is to determine the effect of selection upon genotypes.

The very heart of the pure line theory is the proposi-

[10] Jennings (AMER. NAT., 44: 145, 1910) tells us, "The genotype work lends no support to the idea that evolution occurs in large steps, for it reveals a continuous series of the minutest differences between great numbers of existing races."

[11] Johannsen ("Elemente," p. 356) says in criticism of the Lamarckian theory: "Die Lamarckismus muss kontinuierlich verschiebbare Typen annehmen; wir finden aber bei genauer Prüfung immer und immer wieder Diskontinuität."

tion that selection within the pure line is ineffective.[12] The strenuousness with which this has been maintained has even engendered in some minds the opinion that selection has no rôle at all to play in evolution or in practical breeding. The attitude of many appears to be that Darwin was quite mistaken when he wrote, "The key is man's power of accumulative selection: nature gives successive variations; man adds them up in certain directions useful to him."

Darwin said, "If selection consisted merely in separating some very distinct variety, and breeding from it, the principle would be so obvious as hardly to be worth notice." Fifty years after this was written we hold a symposium to celebrate the discovery that selection is after all merely the isolation of distinct varieties!

Was Darwin right or wrong? Have all practical breeders except those at the oft-quoted Svalöf station been chiefly occupied in wasting their time for the last fifty years? These are very important questions.

The burden of proof obviously lies on the genotypists.[13] Much of the evidence offered is most general and not at all *unzweideutig*. Indeed, when closely analyzed much of the reasoning reduces to a circle of three arcs each of one hundred and twenty degrees:

1. *Definition.*—A genotype or biotype is an organic unit, reproducing itself constantly[14] except for the transitory, non-inheritable modifications due to environmental influence.[15] It is not capable of change by selection.

[12] Johannsen ("Elemente," p. 137) states the problem: "Wird Selektion von Plus—oder Minus—Varianten innerhalb reiner Linien eine Typenverschiebung bezw. eine Galton'sche Regression hervorrufen?"

[13] To be acceptable, the evidence must be quantitative; the observations must either be numerous enough that variations due to uncontrollable factors will average out, or the experiments be conducted with such refined technique that environmental influences are entirely excluded; the statistical reasoning concerning the observations must be logically sound.

[14] "A biotype is a group of individuals which do not differ from one another in any hereditary quality and which therefore constitute a pure race."—Shull, G. H., *Am. Breed. Mag.*, 1: 100, 1910.

[15] "In a given 'pure line' (progeny of a single individual) all detectable

2. *Observation.*—Selection has never been known to produce a change in a genotype. Whenever, as is often the case, selection does result in modification of type this proves that the material considered was impure—that more than one genotype was originally present—or that others arose by mutation, and entirely irrespective of selection.

3. *Conclusion.*—It is therefore proved that selection can not modify the characters of a genotype.

Johannsen has written a very thick and a very convincing-looking book, but if one pins himself down to the task of going from cover to cover he finds that an unfortunate amount of the evidence reduces to this kind of reasoning—in short, to no critical evidence at all.[16] But behind this citing of examples which are not inconsistent with his theory although they prove nothing concerning it; besides this reiteration of testimony which merely excites in the minds of the court-room spectators suspicions concerning the integrity of the defendant without entitling the plaintiff to a verdict before an impartial jury,[17] there are certain direct experimental studies

variations are due to growth and environmental action, and are not inherited.''—Jennings, *Proc. Am. Phil. Soc.*, 47: 521, 1908.

''The standard deviation and coefficient of variation express in a pure race mere temporary conditions of no consequence in heredity. If we could make all conditions of growth and environment the same throughout our pure race, all the evidence indicates that the standard deviation and coefficient of variation would be zero, and this is the positive value of their assistance in determining what shall be the characteristics of the progeny.'' —Jennings, AMER. NAT., 43: 333, 1909.

''Wenn es gelänge, für alle Individuen einer reinen Linie absolut gleiche Lebenslage zu schaffen, müsste die Standardabweichung gleich sein.''—Römer, T., *Arch. Rassen- u. Gesells.-Biologie*, 7: 437–438, 1910.

[16] For instance, he (''Elemente,'' p. 162) refers to the fact that Hallet was unable to improve Le Couteur's wheat, although he had succeeded in improving seventy other samples from all parts of the world, and explains it by the assumption that in every case the seventy series of wheat were mixtures of biotypes while Le Couteur's was a pure line. This may be true, but what is it worth as scientific evidence?

[17] In working over the literature of the pure line theory the lover of fair play is sometimes on the verge of losing his patience, for although the experimental data—at least those which are confided to his reader—upon which Johannsen grounds his own theory are very slender, he is unsparing

which have been adduced in support of the genotype theory. These arguments and the evidence upon which they rest must be examined. For convenience of treatment I do this under three propositions concerning selection, which seem so reasonable that I believe few biologists will feel inclined to deny their soundness. They are at least so reasonable that no worker can afford to leave them out of consideration.

A. Characters which are not Inherited at all can not be Taken to Prove that Selection in General is Ineffective

This is a point of great importance, generally ignored by pure-linists. Biometricians have long known that of the variations of any character whatever not all are inherited.[18] They have also learned that variations in certain characters are not inherited.

Suppose now that one takes a character which gives no correlation between its degree of development in

in his criticism of the pioneer studies which have made his own work possible. Such bald statements as ("Elemente," p. 285), "Alle solche Schlüsse sind aber für die eigentliche Erblichkeitsforschung gänzlich ohne Wert," seem to have little of profit to contribute to science. Johannsen's *ipse dixit* has been taken as gospel. Woltereck (*Verh. Deutch. Zool. Ges.*, 1909: 115) says, "Dieses Resultat erschüttert ernstlich die grundlagen der statistischen Variations; und Erblichkeitforschung, wie sie von die Galton-Pearsonschen Schule betrieben wird." A. Lang (*Verh. Deutch. Zool. Ges.*, 1909: 24) asserts, "Die biometrischen Forschung arbeitet mit unreinen material." Römer (*Archiv f. Rossen- u. Ges.-Biol.*, 7: 427, 1910) tells us, "Variabilitätstudien sind bis in die neueste Zeit meist an Material ausgeführt worden, dessen Einheitlichkeit jeweils als sicher angenommen wurde, das aber nach dem jetzigen Stande der Wissenschaft als unrein angesehen werden muss. Dies tritt besonders hervor bei den veilen Untersuchungen der Biometriker."

[18] This is one of the facts which has led the biometrician to discuss probabilities while biologists in general clamor for certainty in the individual instance. One of the results of recent experimental work that has been hailed with the greatest enthusiasm is that two individuals may be identical in external appearance and yet produce entirely different offspring: in short, that some (somatic) variations are and some are not inherited. The experimental data collected on this point both by pure line and by Mendelian researches are of high value, but those who hail them as novel simply parade their ignorance of much of the pioneer work in variation and inheritance.

parent and offspring in a population and selects to increase or decrease it. He will get no result of selection. If now he takes the same character and selects from the plus and minus variations within a pure line, he will again effect no change by selection. Does either of these cases prove that selection in general is ineffective? Or does the second support in any way Johannsen's genotype theory of heredity? Certainly not.

Certain important work of Pearl and Surface seems to me to deserve mention in this connection.[19] These researches are sometimes referred to as furnishing evidence against the possibility of improvement by selection, and this they do so far as the character with which they have dealt is concerned. In the generalization of their results, however, the greatest caution must be used.

From two series of experiments with the same strain of Barred Plymouth Rock fowls they show that there is little hope of increasing the egg-laying capacity by direct selection for fecundity. These results are doubtless of much practical importance. Biologically they are of interest in confirming the results of other biometric studies which have shown that for man, horse, swine and mice fertility is very slightly inherited in the population. To consider them as indicating that selection in general is ineffective would be a very grave error, for fertility—so far as we may judge from the statistics so far published—seems to be a character *sui generis* in respect to inheritance. To cite these results in support of Johannsen's genotype theory of heredity, as has sometimes been done, is absurd.

Is it not possible that Johannsen's results with beans may be due to seed weight being a character which is not inheritable at all in the population, and which can not, therefore, reasonably be expected to be inherited within the pure line?

[19] Pearl, R., and F. M. Surface, "Inheritance of Fecundity," Bull. Me. Ag. Exp. Sta., 166, 1909. Pearl, R., and F. M. Surface, "Is there a Cumulative Effect of Selection?" *Zeitschr. Ind. Abstamm.- u. Verebungsl.*, 2: 257–275, 1909.

Biologists will agree, I believe, that to test critically the effectiveness of selection in the population and in the pure line, the experimental material must be an apparently homogeneous wild species or a garden variety the individuals of which are not differentiated into subraces by characters other than those under consideration.[20] Conclusions drawn from any experiments in which these simple precautions are neglected seem of doubtful value.

From Professor Johannsen's first memoir, that of 1903, we have no reason to suspect that his material is not, so far as the biologist can judge, homogeneous.[21] We are told nothing of any vegetative differences seen during the two generations grown in 1901 and 1902. Apparently all the numerous reviewers have considered his material perfectly homogeneous except for differentiation into genotypes with respect to seed characters.

In his book, however, one notes with some surprise the casual information ("Elemente," p. 311) that his Pure Line I also has curiously bent seeds, a special "Verhalten" in germination and a "groben Habilus" in the vegetative organs. Indeed Johannsen states that from the form and method of germination, etc., of a seed—even though a strong "minus Abweicher"—he can generally recognize an individual belonging to Line I.

These points should have been made clear at the beginning. If Professor Johannsen's lines really differ in their vegetative characters, so, for instance, that they can be distinguished as they grow in the field, it seems to me that their significance for the efficiency of selection is

[20] Surely we can all agree that the population is to be an apparently homogeneous one, *i. e.*, such that all the individuals would be classified together by a keen taxonomist. If this is not the case, if by definition, "population" means to the pure linist a mixture of several conspicuously different things, there seems little need for further discussion.

[21] Of the seed he says, "Der Ausgangspunkt dieser Untersuchungen war eine gekaufte Partie, etwa 8kg, brauner 'Prinzessbohnen,' wohl eine der altesten Kruppbohnen unten den vielen Kulturformen von *Phaseolus vulgaris*. Die betreffende Ware . . . war ausgezeichnet schön und so gleichmässig, wie es überhaupt hier erwartet werden konnte."

greatly reduced. We do not know to what extent the differences in seed weight which give the low correlation in his population are due to the mixture of races slightly differentiated with respect to their vegetative characters. If this differentiation be considerable, the seed weight character with which Professor Johannsen has chiefly worked, may not be inherited at all in the population providing this population be one composed of individuals with the same vegetative characters. It is not sufficient to be assured that these classic beans differ "nur (oder fast nur)" in seed characters; more detailed information is much needed, and until it is forthcoming I must differ from most biologists in my opinion as to the importance to be attached to the conclusions drawn from them.

B. Improvement for any Single Character can not be supposed to be Unlimited

This is a fundamental consideration too often neglected.[22] A wheat is selected up to its maximum productiveness, perhaps by getting the uppermost attainable limit at one choice from a large field. Then because it can not be made to yield all grain and no stubble we are told that selection can only isolate already existing types. A sugar beet can not be all sugar and the cow can not give pure cream.

In arguing for Johannsen's theory East[23] concludes that since Illinois is no longer making progress in high

[22] The principle, however, has been clearly seen by some biologists. For instance, in his "Foundations of Zoology," Brooks says (p. 165): "A breeder of domesticated animals or of cultivated plants, who devotes his attention to one or two characteristics, must soon reach a point where no further improvement is practicable unless the species is at the same time greatly modified in many other respects." And again (pp. 177–178), "No one can dispute the well-known fact that this sort of *pedigree selection* for a single point quickly grows less and less effective, and soon reaches a maximum; but this is no proof of any 'principle of organic stability,' or anything else except the truth that long ages of natural selection have made the organism such a unit or coordinated whole that no great and continuous change in one feature is possible unless it be accompanied by general or constitutional change."

[23] East, E. M., "The Rôle of Selection in Plant Breeding," *Pop. Sci. Mo.*, 77: 198–199, 1910.

and low oil and protein selection in maize, their work has been merely the isolation of pure and constant strains—"sub-races"—with the characteristics in question as strongly developed in the beginning as we now find them, but continually intercrossing. The case is too complicated for discussion in detail, but certainly the fact that the characters can no longer be increased by selection[24] is no strong argument for the biotype idea. Under its present morphological and physiological organization we have no reason to suppose that the corn grain can be made to contain as much oil as the castor bean.

Again Pearl and Surface[25] announce concerning their selection work with corn,

> We find the results of this experiment or investigation to be very difficult (if not altogether incapable) of rational explanation in accordance with the biological implications of the "law of ancestral inheritance" and conclude that the results agree better with the genotype theory of Johannsen than with that of the cumulative theory of selection with, of course, the limitations implied by the fact that it is an open fertilized plant.

What Pearl and Surface have actually done is to take a desirable sweet corn which they for convenience designate as Type I, and attempt—with initial success—to improve it for yield in ears and stover, for configuration of ears, and especially for earliness. But this Type I corn is descended from a few ears, the offspring of which have been grown in Maine for fifteen to twenty-five years. The variety originally introduced must have been an

[24] That changes due to selection are at first rapid and then slower has long been recognized. Indeed, as early as 1869 Hallett stated as two of his laws of the action of selection, "The improvement which is at first rapid, gradually, after a long series of years, is diminished in amount, and eventually so far arrested that, practically speaking, a limit to the improvement in the desired quality is reached. By still continuing to select the improvement is maintained and practically a fixed type is the result."

Darwin's views on this question are partly expressed in a letter of 1869 to Sir Joseph Hooker ("More Letters," 1: 314), "I am not at all surprised that Hallett has found some varieties of wheat could not be improved in certain desirable qualities as quickly as at first. All experience shows this with animals."

[25] Pearl, R., and F. M. Surface, "Experiments in Breeding Sweet Corn," Me. Ag. Exp. Sta. Bull., 1910.

early one as compared with sweet corn in general, to be able to survive at all in Maine. During the fifteen to twenty-five years the ancestors of the Type I corn were grown in Maine it must have been[26] subjected to an occasional natural selection, for seed could be taken by the farmers from only plants which had ripened their ears. The somatic organization of some plants is such that they require only a few hours for their life cycle, but so long as sweet corn has the general characteristics of root, shoot and leaf that identify it as *Zea Mays* it seems reasonable to suppose that there is some limit to the reduction of the time required for germination, growth and fruiting—an irreducible minimum beyond which selection can not carry it. Surely the fact that Pearl and Surface could not continually reduce the time required for growth while at the same time maintaining a selection for yield of ears and stover may indicate that the irreducible minimum for earliness has been reached in a variety of the physical type they wish to breed. Speaking for myself alone, I must say that the data before us prove nothing against the theory of cumulative effect of selection, and they certainly do not furnish any critical evidence for the Johannsenian theory.

It seems to me that Pearl and Surface again tacitly make this unjustifiable assumption that the modification attainable for any single character is practically unlimited when they consider that their failure to increase egg production by selection is a legitimate argument against the potency of selection. Indeed they say of "200 egg hens," which lay an egg fifty-five per cent. of the days of the year, "This figure is of some interest as indicating what a *relatively* small proportion of the theoretically maximum character is being selected to, when 200-egg birds are bred."[27]

But why, pray, is two hundred and sixty-five and a quarter eggs per year the *theoretical maximum?* One

[26] Judging from the account of the difficulties of growing sweet corn which the authors give us.

[27] Pearl and Surface, Bull. Me. Ag. Exp. Sta., 166: 55.

ignorant of the physiology of reproduction in the domestic fowl might innocently suppose that even a hen needs a rest. If this be true, may it not be that 200 eggs is about the attainable maximum (the physical or physiological limit of the organism) of this variety under the environmental conditions available and that the Maine strain of poultry will not do better than it has? If this is not the attainable limit, why not assume over an egg a day as the theoretical maximum?

C. Selection can not in general carry a Character beyond a Degree Consistent with the Optimum for Maintenance and Reproduction

This proposition is perhaps in a sense explanatory of the one immediately preceding. A characteristic is not independent of, but correlated with the other characteristics of the organism, and if it increases or decreases unduly they must also change or the organism be made more or less unfit for survival.

Have those who claim to have found selection ineffective been selecting against the morphological or physiological balance of the organism, that is in a manner to render the organism less capable of maintenance, growth and reproduction?

If this be true their failure to obtain results will be in some measure explained.

A possible illustration of this case may be furnished by the work of Pearl and Surface on egg production in the domestic fowl. Their work is again chosen not because of any malicious desire to differ from them[28] in interpretation, but because in a brief discussion of the evidence for the genotype theory one must confine his attention to the most important of Johannsen's supporters.

The data are: (*a*) The results of an eight years' selec-

[28] The criticism presented here must not be interpreted as drawing into question the scientific value of the data or the practical importance of the results of the studies criticized, or be extended to other work of the same authors, but is to be limited to the question of interpretation in relation to the pure line problem.

tion for high egg production; (*b*) a correlation between the egg production of thirty-one individual mothers and the egg production of their daughters, and the comparison of the egg production of these daughters with that of a large number of pullets of unregistered female parents.

We note the following details:

1. During the eight-year selection experiment[29] some unfavorable environmental accidents occurred in certain of the laying years. The averages for these years are perhaps too low, and both the actual means and a series of corrected means are given. The corrected means show an insignificant increase, but the unmodified means show a pronounced decrease in mean number of eggs as the result of the eight year selection.

2. In correlating between the egg production of the 31 highly selected mothers and their 217 daughters there is not trustworthy evidence of any relationship between the fertility of the mothers and that of their daughters.[30] *If these constants show any deviation from 0 whatever it is on the negative side.*

3. In comparing the daughters of these "200-egg" hens with three other series of the same strain but not of such highly selected female parentage, both for winter and spring egg production, it is shown that in five cases out of six the offspring of less highly selected parentage are better layers than those of the less stringently selected parents.

Thus all three comparisons indicate that the high laying mothers tend to produce low laying daughters; selection to increase egg production actually decreases it.

[29] "The practise in breeding was to use as mothers of the stock bred in any year only hens which laid between November 1 of the year in which they were hatched and November 1 of the following year, 160 or more eggs. After the first year, all male birds used in the breeding were the sons of mothers whose production in their first laying year was 200 eggs or more. Since the normal average annual egg production of these birds may be taken to be about 125 eggs, it will be seen that the selection practised was fairly stringent." *Zeit. Ind. Abst.- u. Verebungsl.*, 2: 261, 1909.

[30] From a knowledge of the biometric work of the last several years this is just the result which one would have expected to get.

Such a run of results as this can hardly be due to chance.[31] They indicate rather the presence of some as yet undetermined physiological factor.[32]

Candidly viewed and considered in comparison with other biometric work on the inheritance of fertility and fecundity, I think these experiments can not be held to be strongly opposed to the theory of the effectiveness of selection in general. However this may be, they certainly afford no substantiation for Johannsen's genotype theory of heredity.

IV. Summary and Conclusions

By the genotype theory of Johannsen one understands the following propositions:

An apparently uniform population or phænotype is generally not homogeneous, but is composed of a large number of differentiated types, which are to be designated—within limitations to be laid down immediately—as genotypes.

Externally, the genotype can not be distinguished from the phænotype. Both may have normal variation curves, but while that of the phænotype may by proper selection be broken up into constituent genotypes, the variation curve of the genotype can not be modified by selection. In short, the genotype is from the standpoint of heredity a rigid unit. All individuals belonging to the same genotype have the same potencies as parents. Only discontinuous segregations or transformations—mutations—may modify them.

[31] The argument that this observed decrease as the result of selection to increase egg production is due to chance must rest chiefly on one or both of two assumptions. First, that the eight-year selection experiment is absolutely untrustworthy because of the accidents which may have affected the egg production in certain years adversely. Second, that 31 mothers is a number entirely too small to give significant results in the case of a character like fecundity. These admissions would vitiate entirely any conclusion concerning selection to be drawn from these experiments.

[32] To me it seems that some of Pearl and Surface's published data are most suggestive of the nature of this factor, but they doubtless have in progress experiments that will throw light on these matters and biologists will await their results with interest.

The keystone of the pure line arch is the proposition that selection is ineffective except as a means of separating already existing genotypes. If this keystone-proposition be not sound the whole structure of the theory crumbles.

The propositions of the genotype theory are such that scientific proof or disproof is rendered particularly difficult. By theory selection can not effect a change in a pure line; by a slippery process of reasoning in a circle any results attained by selection are at once discredited by the assertion that the original material was impure. If, on the contrary, any selection experiment is ineffectual it is by some process of reasoning quite incomprehensible to some of us, at once chalked up to the credit of the new theory. If heritable differences appear within a pure line known to be so, these results are also discredited by the assertion that the observed change is a mutation or has been produced by the action of the environment. Truly the unbiased investigator is between the devil and the deep sea!

The actual experimental data upon which the genotype theory rests are as yet few. Johannsen's conclusions for beans depend chiefly upon the offspring of only nineteen seeds, and so far as I am aware no other investigator has confirmed his results on *Phaseolus*. Hanel had only twenty-six original *Hydra*, and Pearson's analysis of his data with more adequate methods than he used, evidences against rather than for the genotype theory. Jennings gives us the records of only six selection experiments involving altogether only a few actually selected *Paramecia*. Considering the large environmental and growth factors, his conclusions can not be considered as beyond question.[33] The work of Pearl and Surface with poultry and maize seems to me to have

[33] In offering this criticism I wish to express the highest admiration for Professor Jennings's two memoirs on variation, heredity and evolution in the protozoa. The coupling of refined statistical with careful experimental methods in the investigation of these organisms marks a great advance in biology.

no critical bearing on the pure line problem.[34] This is also true of numbers of other smaller experiments which can not be cited.

If one turns from the strictly pure line side of the problem to the more general questions of the "something" or "Etwas" in the germ plasm which determines in large degree the somatic characters of the individual which develops from it, one can only suggest that nothing whatever is explained by giving another name to a well-known fact. Ever since the time of Darwin, and before, we have known that there was "something" in the germ cells which determined the character of the offspring. We have had a dozen different names for this something, and by adding a thirteenth, "Gene," Johannsen has merely burdened us with another cloak for our ignorance. Unfortunately biological closets are full of such cloaks, once in fashion—now out.

Finally, I must make my own position quite clear. With Professor Jennings's contention that pure line cultures are of fundamental importance in many fields of physiology and genetics, I am in hearty agreement. Like other breeds of facts, "pure line facts" can not become too abundant. Indeed, *a priori,* I am not opposed to the genotype theory. As a theory it is most attractive, but one can not accept it without proof on that account. Personally, I am one of "that last small remnant" who believe that in a problem of this kind the proof must be biometric. This means merely three things. In so far as the nature of the material permits, all the data considered must be quantitative. The data must be numerous enough that biological relationships will not be obscured by the errors of random sampling. The data must be analyzed by logically sound methods.

Judged by these standards, I must express the conviction that as yet there is no adequate justification for the genotype or pure line theory.

[34] Naturally, this is purely a matter of interpretation, and does not diminish in the slightest degree the value of the work.

THE INFLUENCE OF CHANGED EXTERNAL CONDITIONS ON THE DEVELOPMENT OF TWO SPECIES OF MOTHS

PROFESSOR THOMAS H. MONTGOMERY, JR.
UNIVERSITY OF PENNSYLVANIA

THESE experiments were carried out in the fall and winter of 1908–09, and their results are not without interest even though no marked changes in the insects were effected.

I. *Attacus cecropia* LINN.

Cocoons of this large Saturniid were collected in New Jersey in December and January. The controls, kept in their cocoons, were hung out-of-doors exposed to rain and sun until the latter part of April, then placed in a hatching cage in a room at out-of-doors temperature, when they hatched in May. The pupæ to be experimented upon were removed from the cocoons and kept in horizontal positions unless otherwise specified.

A. *Experiments with Light*

Direct Sunlight.—Four pupæ, lot no. 86, of which only one was healthy in appearance, were placed in direct sunlight in a warm room (21° C.) on February 5; one of them hatched on February 10 and laid eggs, while the other died. Evidently direct sunlight is not fatal to them.

Direct Sunlight behind a Heat Filter.—Twenty pupæ, lot no. 83, were laid horizontally on their dorsal surfaces with heads directed towards the sunlight, behind a vertical flat glass jar containing a saturated aqueous solution of alum, in a warm room (21° C.). They were thus placed on January 22, and all hatched in March following.

Diffuse Sunlight.—Five pupæ, lot no. 65, were placed, each vertical with head up in a test-tube in a room that never sank quite as low as freezing; all hatched between May 15 and June 2.

Five pupæ, lot no. 66, were kept under similar conditions, but placed with their heads down in the test-tubes; four of these hatched in May, the fifth being infected by parasites. Three pupæ, lot no. 69, were placed vertically in separate tubes within a moist chamber near a steam radiator in my private laboratory; two hatched in February, the third died.

B. *Experiments with the Tracheal Stigmata Covered*

Twenty pupæ, lot no. 85, were placed in a warm room (21° C.) in diffuse sunlight. On January 22 the stigmata, of which there are eight easily recognizable pairs counting those of the head, were covered with a gum-arabic solution, but this peeled off and was replaced the next day by pure Canada balsam. It is, however, quite doubtful how efficient the balsam was in excluding air from the respiratory tubules, for it does not adhere very well to the greasy surface of the cuticula. Four of these pupæ, lot 85A, had seven stigmata of the right side covered, and all hatched. Four others, lot 85B, had the first pair of stigmata covered, and all hatched. Four others, lot 85C, had the second and third pairs of stigmata covered, and all hatched. Four others, lot 85D, had the sixth and seventh pairs covered, and three hatched. Four others, lot 85E, had the fourth pair covered, and three hatched.

C. *Experiments with Higher Temperatures*

Ten pupæ, lot no. 68, were placed within a closed and dry glass jar in diffuse light, kept thus at 28° C. for 23 days, then removed from the jar and kept in diffuse light in a room at 21° C. All hatched, except three that were parasitized.

Twenty-two pupæ, lot no. 80, were placed on January

5 in an egg incubator at 39° C., kept there for varying periods, then removed into a warm room (diffuse light, 21° C.) until hatching. These were divided into lots as follows:

80A, 4 pupæ, incubator 1 day, all hatched in March.
80B, 3 pupæ, incubator 2 days, all hatched in February and March.
80C, 3 pupæ, incubator 3 days, 2 hatched in March.
80D, 3 pupæ, incubator 4 days, all hatched in March.
80E, 3 pupæ, incubator 6 days, 2 hatched in February.
80F, 3 pupæ, incubator 7 days, all hatched in February and March.
80G, 3 pupæ, incubator 28 days, all hatched in March.

Twelve pupæ, lot no. 84, were placed in an egg incubator from January 22 to February 18, then removed to diffuse light in a warm room (21° C.) for hatching; the temperature in the incubator was 39° C. until January 28, after that 39.5° C. Nine of these hatched in March and April.

D. *Experiments with Lower Temperature*

Seven pupæ, no. 41, were placed in a tight covered and dry glass jar in an ordinary ice refrigerator from December 7 to March 29, afterwards removed to a warm room; three hatched May 17, the others were destroyed by an accident.

Thirteen pupæ, no. 67, were treated similarly; two hatched on May 17, the others were killed accidentally.

E. *Results of the Experiments*

The pupæ were exposed to unusual external conditions: removed from the cocoon, exposed to direct sunlight with and without a heat filter, to diffuse light, to various temperatures ranging from 0° C. to 39° C., with the stigmata covered with balsam, in horizontal and vertical positions. Yet nearly as great a proportion hatched as in the case of the controls. Higher temperatures hastened the rate of development. Further, the pupæ so abnormally treated did not differ in coloration from the controls or to no extent that could be measured;

this result applies to the pattern as well as to the intensity of the coloration. For in the controls quite as great a range of color variation was found as in the others. Also the unusual conditions of life did not appear to effect the dimensions of the hatched moths. To decide this I took as the most convenient measurement the length of the fore wing, measured from its point of insertion against the thorax to the most anterior edge of a dark spot placed anteriorly near the apex of the wing; I did not measure to the extreme free edge of this wing, for that portion is very flexible and liable to become folded during the process of mounting the moths. The right wing was measured unless it happened to be misshapen. Only about a hundred moths were preserved, too few for any statistical study of this wing length, consequently in the following table only the extremes of variation of this length are given (expressed in millimeters, and accurate to within a half millimeter).

Lot 40 (1♂, 5♀) control	♂ length 67.5	♀ length 69.0–74.5
Lot 64 (2♂, 6♀) control	♂ length 61.0–65.0	♀ length 61.0–75.5
Lot 68 (4♂, 3♀)	♂ length 58.0–64.0	♀ length 64.0–73.0
Lot 69 (2♂)	♂ length 66.0–67.0	
Lot 79 (3♂, 3♀) control	♂ length 59.5–65.0	♀ length 69.0–75.0
Lot 80 (7♂, 7♀)	♂ length 61.5–70.0	♀ length 61.0–73.0
Lot 82 (3♂, 6♀) control	♂ length 67.0–69.0	♀ length 66.5–74.0
Lot 83 (12♂, 6♀)	♂ length 60.0–68.5	♀ length 67.0–73.0
Lot 84 (2♂, 4♀)	♂ length 67.0–67.5	♀ length 68.0–71.5
Lot 85 (12♂, 3♀)	♂ length 63.0–69.0	♀ length 65.5–73.0

It is probable that this late pupal stage is so advanced in its development that it can not become much modified by external changes.

II. *Thyridopteryx ephemeræformis* Steph.

This psychid is the common "bag-worm" or "basket-worm." The larva immediately on hatching constructs a bag or cocoon of silk covered with portions of leaves or chips, and increases the size of the bag as it grows and carries it about. At the end of the summer each attaches its bag firmly to the twig of a tree, and the male

emerges as a winged insect; probably the male does not overwinter. But the female neither forsakes her bag nor acquires wings, she is impregnated by the male within her bag. Each female produces a large number of small eggs but does not oviposit, for she dies within her bag and her dead body becomes a case for the eggs; at her death her viscera change into a soft cottony mass that acts as a further protection for the eggs. Among some 200 cocoons collected on November 24 I found about half a dozen in which the egg case, the degenerate female, was still living. This species is then a very favorable insect for obtaining eggs and early embryos in large abundance during the colder season of the year, and should prove a valuable object for experimentation.[1]

The controls were kept within their cocoons out-of-doors, and hatched in the end of May. In the experiments sometimes the eggs (in early embryonic stages) were removed from the egg cases, sometimes kept in them.

A. *Experiments with Sunlight*

Direct Sunlight.—Lot no. 77, collected January 4, consisted of egg cases placed in closed dry bottles in the south window of a warm room (21° C.). 77C, kept three weeks in this sunlight, did not hatch; 77A, an untimed period in sunlight, hatched. Lot 78, collected January 4, consisted of freed eggs in corked vials without moisture, with similar exposure to the light; they were divided into four lots, placed in the sunlight for 3, 7, 10 and 14 days respectively, and all hatched about March 1.

Direct Sunlight behind an Alum Heat Filter.—Four lots of freed eggs (nos. 51, 53, 49, 50) collected January 4 were used, placed in the sun behind a heat filter for 2, 7, 18 and 28 days, respectively, and all hatched in January.

[1] A good popular account of this species is given by McCook: "Tenants of an Old Farm," New York, 1885, and this is illustrated with excellent figures. But he makes the common mistake of other naturalists in supposing that the female oviposits. See also Howard and Chittenden, circular No. 97, U. S. Department of Agriculture, 1908.

Diffuse Sunlight.—A considerable number of lots of egg cases and freed cocoons, collected November 4, were placed in diffuse north light in a warm room (21° C.), and all hatched in January and February.

B. *Experiments with Colored Light*

Freed eggs, collected November 4, were placed within vials immersed in colored solutions within larger bottles, the vial passing through the cork of the larger bottle and held by it. The solutions employed were: acid fuchsine in 50 per cent. and 70 per cent. alcohol; Berlin blue in distilled water; safranine O in 95 per cent. alcohol; orange G in 50 per cent. alcohol; eosine in 70 per cent. alcohol; methylen green in distilled water; picric acid in 50 per cent. alcohol; scarlet 12 gm. in 1,000 c.c. water, this last giving monochromatic light.[2]

In Sunlight behind an Alum Filter, then removed to diffuse light in a warm room (21° C.). Lots 43, 46, 47 were immersed in a scarlet solution, as follows:

Lot 43 in sunlight 4 days, hatched January 15.
Lot 46 in sunlight 28 days, hatched January 9.
Lot 47 in sunlight 32 days, hatched January 11.

In Diffuse North Light.—The following experiments were made in a breeding room of which the temperature was a few degrees above that out-of-doors. Two different lots were raised in a fuchsine solution, one in safranine, one in orange G, one in eosine, one in picric acid. All hatched in May.

Others were placed in a room at 21° C. One series were immersed in a fuchsine solution for 7, 18, 28, 35 days, respectively, then removed to ordinary daylight; these hatched in the latter half of January and first half of February. Others were kept continuously immersed in the following solutions: Berlin blue, methyl green, scarlet, and these hatched in the first part of February.

[2] Vide Pennington, W. E., 1897, "A Chemico-physiological Study of *Spirogyra nitida*," Publ. Univ. Penna. Contr. Bot. Lab. 1.

C. *Experiments with High Temperatures*

Freed eggs, from cocoons collected November 4, were placed in an egg incubator at 39° C. for varying periods, then removed to the dark of an ordinarily warmed room (21° C.). Those kept in the incubator for periods of 1, 2, 3, 4, 5, 7 days hatched in February; those kept in the incubator for eight and eleven days did not hatch.

Ten unopened cocoons and ten egg cases placed in a dry covered slide box, and ten egg cases placed in a dry closed jar, all at 32° C., did not hatch. Five egg cases placed in a moist chamber at 28° C. hatched December 15 (these had been collected November 24). Four other egg cases, treated like the last but with less moisture, hatched in January.

D. *Experiments with Low Temperatures*

Six egg cases were placed out-of-doors in a closed tin box, protected from the rain. They hatched, as was to be anticipated, at the same time as the controls.

Fourteen egg cases were placed in a closed jar within an ordinary refrigerator from November 24 until March 29, then removed to a warm room (21° C.); these also hatched at the same time as the controls.

E. *Results of the Experiments*

I tried to raise the small hatched larvæ by placing them upon arbor vitæ within a moist chamber; but owing to the great time consumed in transferring them to fresh pieces of the food plant, I was obliged to relinquish the attempt, and they all died. Consequently I did not determine whether those hatched under the abnormal conditions differ from control larvæ of the same age.

The eggs of this species develop into larvæ under direct sunlight with and without a heat filter, in diffuse light, in all the colored lights employed, at a temperature of 39° C. provided it be not continued longer than seven days, as well as at temperatures at and slightly below freezing. But what seems to be a necessary con-

dition for development is a certain amount of moisture, for the insects die when subjected to higher temperatures within dry vessels. The main effect of increase of temperature seems to be to hasten the rate of development. Probably it is the relative thickness of the chorion of the eggs that proves their chief protection under changed external conditions.

The experiments on this moth and on *Attacus* would show that the cocoon can have no particular value by excluding the sunlight, for we have found that sunlight is not injurious to the eggs and pupæ. Probably the main value of an insect cocoon is that of protecting against enemies, though it may also be of service in preserving a proper amount of moisture; for cocoons soak up the rain and melting snow, and would retain it for a considerable while.

SHORTER ARTICLES AND DISCUSSION

THE ONTOGENY OF A GENUS

In the systematic work of to-day there is noticeable a tendency toward undue magnification of the importance of the smallest units, the species, subspecies, varieties or whatever they are called, to the great detriment of the larger and more important units, the genera, families and higher groups. While there is a very general agreement among systematists as to what constitutes a species or a subspecies or variety, the concept of a genus is found to vary widely; we have not yet brought ourselves to see the necessity of bestowing that care upon the genera which we use in the study of species and minor divisions. Yet after all the genera and the families are the units of paramount importance, for they are the units with which the majority of workers must eventually deal. Zoology has become such a vast field that he who would occupy himself with species must of necessity restrict himself to a very small section of the animal kingdom.

It has therefore become essential for us to examine the characteristics of natural genera, and to analyze them carefully in order that we may discover certain general truths which will aid us in determining what genera are logical and valid and what are mere artificial aggregations, brought together solely for the sake of convenience.

As commonly accepted, a genus is a group of species which is separated from all other similar groups of species by some character common to all the component units, the latter being differentiated *inter se* by the unequal development of the specific, or, more accurately, intergeneric variables. In case a group of species uniformly differs from another similar group in the majority of the characters available for systematic purposes, that group is properly considered a family or a subfamily.

Immediately upon its appearance, a genus (at this stage merely a vigorous species) spreads in every direction just as far as it is possible to maintain itself, that is, until it encounters on every side insurmountable barriers. But the conditions found throughout this habitable area are not uniform. This causes many local races to develop, each grading insensibly into all those surrounding it. Thus a genus in its infancy is in reality a well-marked species, differentiated into many geographical races.

These races do not long maintain themselves in their original relationships. There is somewhere within the range of this young genus, normally at or near the center, an area of optimum conditions, where life is easy and there is no severe struggle for existence. Here various more or less aberrant types arise and are able to perpetuate themselves, spreading out in every direction as did the original stock, but never so far, as they are not so well prepared to encounter adverse conditions. Thus in the second stage a genus is in reality a well-marked species, differentiated into many geographical races, and in the center of its range being accompanied by several additional closely allied species.

After the formation of these several supernumerary species, each usually with a few races of its own, the genus soon reaches maturity. Each of the numerous component forms increases in numbers so that in its own little sphere the struggle for existence becomes acute, and any variation from an arbitrary type is unable to maintain itself. The forms occupying the limits of the range of the genus as a whole (geographical or bathymetrical) are continually trying to colonize new territory, both from their own initiative and as the result of pressure from behind. This encounter with generically unfavorable conditions induces, in the border forms, a more or less pathological condition, inducing great individual variation; and so we normally find that the species which occupy the outer borders of the area inhabited by the genus as a whole, just as in any species the individuals from the edge of the area inhabited by it, are much more variable than those from any other part.

If we take the species of any genus which has reached the stage of maturity just described and arrange them according to the proportionate value of their specific characters, we find in the center a single species, or a group of closely allied species, whose range is coterminal with that of the genus as a whole. This species is, moreover, typically the most variable of any in the genus, and probably is very close to the original stock.

The period of maturity being passed, senescence begins to assert itself. By long existence under fixed conditions the various component species become, as it were, delicate, and are unable to withstand any changes in their environment. Such changes are, however, of constant occurrence, affecting greater or lesser areas; and therefore discontinuance of distribution creeps in, species being cut off from the main zoogeographic area inhab-

ited by the genus, one by one, by the extirpation of the intermediate forms. It often happens, also, that changing ecological conditions at the center of distribution of the genus, such as the local development or introduction of predaceous forms, or of external or internal parasites, destroys the typical form there, leaving only aberrant types; or they may even obliterate all traces of the genus.

Very old genera are thus characterized by having but few species in widely separated localities, each widely different from the others. These are usually (and rightly) regarded as representing a family composed of a few monotypic, or nearly monotypic, genera.

Very often old genera undergo what has aptly been termed an "explosion" of the intergeneric characters, and are then composed wholly, or almost wholly, of curious and eccentric species; again a genus in its senescence often is marked by a great development of certain characters at the expense of others, which usually leads to prompt extinction. In certain localities large numbers of species are remarkable for their eccentric development, and the exaggeration of certain characters out of all proportion to the others, which, so far as we can see, serves no useful purpose. Such localities from a zoological point of view must be considered as old and to have persisted in their present state beyond the normal life cycle of the genera which have given rise to the erratic species. Just as the life cycle of different animals varies enormously, so does that of species and of genera. Scores of genera belonging to the higher groups of the animal kingdom may arise, grow strong, decline, and finally, with a grand "explosion" of their characters, disappear, before a genus belonging to one of the lower groups, of earlier origin, has reached the summit of its strength.

In discussing genera, as well as species, one must always keep in mind that for all animals there are two, and for aquatic animals three types of distribution, viz., (1) geographical, with purely inorganic physical barriers; (2) ecological, with wholly organic barriers, consisting of presence or absence of food and predaceous or parasitic enemies; and (3) bathymetric, again with purely physical barriers of pressure and temperature, the latter commonly being the more important with lower animals, the former with the higher.

AUSTIN HOBART CLARK.

U. S. NATIONAL MUSEUM.

NOTES AND LITERATURE

RECENT CONTRIBUTIONS TO A KNOWLEDGE OF THE EXTINCT AMPHIBIA

THE past few months have witnessed an unusual activity among paleontologists in behalf of the extinct Amphibia. There have been several rather extensive papers and an important memoir on the group issued within the last twelve months. It is to be hoped that many other investigators will come to be interested in this group of vertebrates, for it is only by descriptions and discussions that we shall ever attain any adequate conception of the relationships of these highly interesting and important forms. The writer is of the opinion that the present conception is capable of considerable improvement and in order to facilitate this improvement he offers a review of the recent literature on the group.

Dr. A. Smith Woodward (1) has described an interesting new amphibian from the "Oil Shale, at Airly, New South Wales." Dr. Woodward locates his form in the genus *Bothriceps* of Huxley. The skull and greater part of the vertebral column with the ribs and a portion of the right arm are preserved. It is described as a new species under the name *Bothriceps major,* but as this term had already been used by Lydekker for the reception of the uncertain *Petrophryne major* of Owen[1] it will be necessary for the Australian specimen to receive a new name, for which the term *Bothriceps woodwardi* would not be inappropriate. Dr. Woodward allies the form with the Archegosauridæ, but the reviewer is rather inclined to think that the Tuditanidæ would be its nearer relatives. This is the third form described from the Hawkesbury formation of New South Wales. Further search will undoubtedly reveal other Paleozoic amphibia. It will be noticed in this as in so many other Paleozoic localities where fossil amphibia are found, that nearly every new specimen represents an unknown form, thus indicating the diversity and age of the group. The known species from the Hawkesbury formation are: *Bothriceps australis* Huxley, *Bothriceps woodwardi* and *Platyceps wilkinsoni* Stephens.

Dr. S. W. Williston has described in some detail (2) the

[1] Cat. Fossil Amphb. and Rept. Brit. Museum, Pt. IV, p. 174.

remains of *Dissorophus multicinctus* Cope which has recently been recovered from the reputed Permian of Texas. His material greatly increases our knowledge of the genus and of the anatomy of the Permian amphibia. He describes a complete skull, in which, unfortunately, the sutures are not discernible. Nor are the lateral line canals to be found, a fact to be regretted since we shall undoubtedly be enabled to base considerable importance on these structures did they occur. The skull roof is pitted like all other of the Permian amphibia from Texas. A large portion of the carapace is described with its attached vertebræ. The dermal shield is broad, continuous and pitted, forming a covering over the thoracic region of the animal. Limb bones, a scapula and a portion of the interclavicle are described. The form is closely related to another animal recently described by Dr. Williston and the two are placed in the new family Dissorophidæ. The paper closes with a taxonomic list of the Permian amphibia from Texas for which paleontologists will be grateful. There are three orders, nine families and thirty-four species so far known in the fauna.

The same writer has described (3) a nearly complete skeleton of a new temnospondylous amphibian from the Texas Permian. The form is very remarkable in several of its characters. The following are the chief unusual characters of the new genus: a median unpaired rostral opening leading into a palatine vacuity, greatly enlarged antorbital vacuities, temporal fenestræ, apparent absence of the parasphenoid bone, osseous carpus and tarsus and the possession of short heavy ribs borne on transverse processes. The skeleton is greatly similar to that of *Eryops,* but the skull shows decided differences.

The temporal fenestra is not homologous to the superior temporal fenestra of reptiles, but it is rather to be considered as a greatly elongate and closed epiotic notch. The median unpaired rostral opening is similar in structure to the one found in the skull of *Dasyceps bucklandi* Lloyd from the Permian of Kenilworth, though in the present form the opening is much further forward and smaller. The antorbital vacuities in the present form, on the other hand, are much larger than the same openings in *Dasyceps.*

Dr. Williston was able to make out the complete anatomy of the skull and has figured it in three views. The most remarkable feature of the palatal structure is the apparent absence of the parasphenoid. The vertebral formula is 22 for the presacral vertebræ, an uncertain number of caudals and a single sacral. The

sacral rib is much like that of *Eryops* in which the structure takes a very unusual form for a rib. The phalangeal formula for the foot is 1, 2, 3, 4, 2. The complete number of digits in the hand is not preserved. The carpus has nine possibly eleven osseous elements, and the tarsus has twelve osseous elements.

The paper is well illustrated. There is a restoration of the skeleton of *Trematops milleri* and an outline drawing of the scapula of *Eryops latus* Case. The new genus *Trematops* is the type of a new family Trematopsidæ in which the form described by Cope as *Acheloma cumminsi* is doubtfully associated.

The same writer (4) has redescribed from more complete material the species named by Cope as *Diplocaulus limbatus* from the Permian of Texas. The paper is based on several more or less incomplete skeletons. These include several additional features to our knowledge of the anatomy of the peculiar Diplocaulidæ. Limbs have heretofore been unknown in the group although their presence has been suspected from the presence of pectoral girdles preserved with some specimens. Dr. Williston, however, for the first time actually describes well-formed limb bones for the group. The humerus is very remarkable in that it has an epicondylar foramen, a character known in only one other amphibian, *Acheloma*. The complete morphology of the skull with the exception of some features of the palate are made out and represented in two plates. The clavicular girdle, mandible, vertebræ and limb bones are represented in other plates. The paper concludes with remarks concerning the relationship of the group to which *Diplocalus* belongs and associates the Oklahoma Permian form *Crossotelos* with the *Diplocaulus*. He remarks that in the Microsauria the capitulum of the rib is always attached intercentrally and suggests that *Diplocaulus* must be retained among the Microsauria.

The same writer (5) has given an extensive paper on new Permian forms in which he describes a new genus and species of amphibia under the name *Cacops aspidephorus*. This form he locates in the family Dissorophidæ. The paper opens with a brief discussion of the "Character of the Permian Beds of Northern Texas," "Conditions of Fossilization" and "Associated Vertebrates." The form described in the paper is represented by a skeleton which is remarkably complete "with no more plaster in its construction than was necessary to cement the freshly broken parts . . . save of many of the phalanges. . . ." It was so complete and well preserved as to be capable of being mounted like a recent skeleton which has been well executed by

Mr. Paul Miller with remarkable success. A photograph of the mounted skeleton is given in one of the plates.

There are four skulls. The most remarkable feature of the dorsum is the presence of a closed otic notch which resembles a temporal fenestra. In none of the skulls was it possible to determine the sutures and the structure of the skull had to be determined more by topographic features. The structure of the palate is of the stegocephalian type, though remarkable in some of its features, such as the large size of the palatal openings. The vertebræ were preserved practically complete and the vertebral formula is—presacral, 21; sacral, 2; pygals, 6, and chevron caudals, 15 or 16. Fifteen of the vertebral spines are elongated and expanded and serve to support a carapace of shield-shaped, scute-like plates which overlap shingle-like. They greatly resemble in structure the dermal plates of *Dissorophus*. A discussion of the "carapace in allied forms" is given and the dermal elements of *Aspidosaurus, Zatrachys, Dissorophus* are discussed. Plates are suggested by the expanded neural spines of *Euchirosaurus* and *Eryops*.

The vertebral column is fully discussed. This includes some unusual features, such as two sacral vertebræ and a well-preserved atlas which is composed of a single piece. The writer discusses also the significance of the hypocentra and pleurocentra, one of the most perplexed questions in connection with the extinct amphibia. The pectoral girdle consists of the fused scapula-coracoid, a cleithrum, clavicles and interclavicle. The humerus and its use in diagnosis is discussed at some length. Among the material studied are many humeri, some of which suggest unknown forms of amphibia. Two new families, the Trematopsidæ and Dissorophidæ, are proposed and the characters given. The paper closes with a discussion of the restoration of *Cacops* and the description of a peculiar form of reptile in which the vertebræ are intermediate between what is known in temnospondylous amphibia and reptilia.

The same writer (16) in a discussion of the faunal relations of the early vertebrates, presented before Section E of the American Association in 1909, gives the relations of the American Permian and Carboniferous amphibian faunas with those known elsewhere. He reaches the conclusion that the Permian fauna is especially isolated. In his discussion of the Microsauria he says, "It has been assumed on entirely insufficient evidence that they too were all amphibians"—and later: "We may be assured that some of them before the close of the Pennsylvanian were inhabit-

ants of high-and-dry land regions where fleetness of movement, rather than obscurity, preserved them from their enemies, crawling reptiles in everything save some insignificant technical details of their palates." This has been recognized by many students of the fossil amphibia and Gadow placed them in a new group which he has called Proreptilia, but his classification does not seem to have been accepted. Dr. Williston says further, "Specialization of the microsaurs had reached the extraordinary extent of snake-like limbless forms." These snake-like forms have been usually associated in another order, the Aistopoa, but the reviewer has shown elsewhere that the group is a heterogeneous one and is made up of specialized microsaurian forms of diverse relationships.

Dr. E. C. Case (6) has described three, perhaps four, new forms of amphibia from the Permian of Texas. The forms as a whole are very insufficiently described. One species, *Trimerorhachis alleni* is described in ten lines and no figure given. This manner of descriptions should be subjected to the severest criticism as it imposes many heavy burdens on the shoulders of succeeding workers. The new genus *Tersomius* is not defined at all. While we may not doubt that the genus is new, judging from the single outline figure, yet it would have been much better, for those who are not so well acquainted with the Permian fauna as is Dr. Case, had he given in what ways it differs from the other amphibia. He allies the genus with *Trimerorhachis* at least so far as resemblances are concerned. The new genus and species are given in fifteen lines of less than ten words each.

A new form, *Gymnarthrus willoughbi*, is much better described. Its relations are uncertain. Dr. Broom allies it with the amphibia, but Dr. Case does not regard the form as such. He remarks its close alliance with *Cardiocephalus sternbergii*, which is amphibian. If *Gymnarthrus* is not amphibian it is certainly a very remarkable amphibian-like reptile.

Dr. E. B. Branson (7) has described and figured, in an excellent photograph, footprints of possible amphibians from the Mississippian rocks of Giles Co., Virginia. Five well-preserved tracks are represented in the figure. The author proposes the new specific name *Dromopus aduncus* and gives a list of the amphibian footprints known from the Mississippian.

The most notable attempt on the part of paleontologists, to elucidate an entire amphibian fauna, is that of Armand Thevenin (8) in the most important memoir on fossil amphibia for many months. The National Academy of France awarded him a prize

for the presentation of the memoir. The paper was published in successive issues of the *Annales de Paleontologie* and in complete form contains sixty-three quarto pages and nine photogravure plates, illustrating all that is known of the Paleozoic amphibian fauna of France up to the present.

The author divides the amphibian forms into four groups: the Phyllospondyles, which is a subordinate group of the "Stegocephales"; the Temnospondyles: the Aistopodes, and the Microsaurians, which unfortunately he ranks in with the reptiles, and describes under this heading a form which a few years ago he had concluded was a rhynchocephalian. Dr. Williston was more inclined to regard it as a Cotylosaurian. Whatever reptilian group it belongs to the reviewer is unable to say, but he is quite certain it is not a Microsaurian.

Dr. Thevenin discusses, under the heading, Phyllospondyles, the forms *Protriton fayoli* Thevenin, *P. petrolei* Gaudry, and *Pelosaurus laticeps* Credner. The second group consists of *Actinodon brevis, A. frossardi* and *Euchirosaurus rochei.* The Aistopodes are represented by a single new form which is unnamed. The specimen strikingly suggests the snake-like amphibians of Ohio and Ireland. There are no true representatives of the Microsauria known in France.

Our author discusses some general questions in regard to the amphibia, such as—"the relations of the Autun amphibia to those of other countries," "the homologies of the temnospondylous and the phyllospondylous vertebræ," "homologies of the elements of the pectoral girdle," "the ancestry of the Stegocephalia" and "the descendants of the Permian Stegocephalia."

Nothing new is added to our previous knowledge of the complex relations of the elements of the temnospondylous vertebra, which is one of the most vexed and most discussed questions in connection with the extinct amphibia. His homologies of the elements of the pectoral girdle are the ordinary interpretations. The ancestors of the Stegocephalia are possibly the crossopterygian fishes, although this is no new conclusion nor does our writer claim this. Perhaps the crossopterygians will do as well as anything. At least they will serve until we find what the *real* ancestors were.

In a discussion on "the descendants of the Permian Stegocephala" he concludes that the branchiosaurian forms were the ancestors of the modern Urodeles and that the Temnospondylia gave rise to some of the reptiles, possibly some of the Cotylosauria. Our author, on a later page, gives the stratigraphic dis-

tribution of the amphibians and reptiles of the Permian of France. His final conclusion is that the diversity of the reptiles and amphibians shows that the groups had arisen long previously and the existence of similar forms in Europe and America would indicate some land connection of the two continents during the Permian.

Dr. Friedrich von Huene has redescribed the skull of *Dasyceps bucklandi* (Lloyd) (9) from the Permian of Kenilworth. This skull was previously studied by Huxley, but rather inadequately described. After a careful description of the elements of the skull Dr. Huene locates the form in the family Melosauridæ, although the form has characters which are unusual for the other members of this group. He discusses the character and significance of the "facialgrube" or internasal opening, which has been described in another Permian form by Williston. Huene finds the same opening occurs in many living urodeles and lists nineteen species in which the opening has been described. He says that it has also been observed in certain members of the Permian Microsauria described by Fritsch from Bohemia. Its significance is possibly the same as in the living amphibia, that of receiving the glandula intermaxillaris. Since this gland in living land-dwelling amphibia secretes a sticky substance used in capturing insects, Dr. Huene suggests that perhaps *Dasyceps* also captured insects. This may, of course, have been possible, but to the reviewer it suggests a greater activity than could be expected of such a sluggish creature as *Dasyceps* undoubtedly was, since it would require many insects to feed an animal three or four feet long and it would be necessary to secure them in some quantity. Dr. Huene suggests that the insects "im Perm und Carbon sehr bedeutende Grössen erreichten"; such was undoubtedly the case with a few species, but the great majority of insects of the Carboniferous and Permian do not greatly exceed the modern insect fauna, so that Dr. Huene's argument on that score is not a good one. *Dasyceps* was probably a land animal and Dr. Huene thinks this is indicated by the presence of the internal opening which occurs only in the land-inhabiting forms among recent Amphibia. Perhaps the analogy may be carried so far.

Dr. R. Broom (10) compares the Permian amphibian fauna of North America and Europe and finds little similarity. He regards the American types as more highly developed. He divides the Permian amphibia of North America into four groups.

He discusses again the relationship of *Lysorophus* and in his discussion quotes the reviewer as saying what he did *not* say. The point of the reviewer's criticism of the reference of *Lysorophus* to the Urodela was *not* the presence of ribs nor yet the snake-like character which Dr. Broom explains in a very elementary way, but it was the *character* of the ribs. Their long, curved condition is unknown among other Caudata and the reviewer does not feel satisfied that *Lysorophus* is a Urodele even though limbs should be discovered.

Dr. Broom suggests for the newly described *Gymnarthrus* of Case an amphibian relationship. The dorsum of the skull shows characters, however, which apparently ally it with *Pariotichus*.

Dr. Broom's other essay (11) on practically the same subject matter gives the additional suggestion that the American and African amphibia are "two different modifications of the same earlier fauna.'

Mr. Robert Dunlop (12) has given some interesting notes on Carboniferous and other Paleozoic amphibia of Scotland contained in the Kilmarnock Museum before they were destroyed by fire. His notes are accompanied and illustrated by two excellent half-tone plates of photographs of type specimens of *Loxomma, Pteroplax* and *Anthracosaurus*, all of which is very welcome information.

Jaekel (14) has proposed a new classification for the Chordata which he calls Vertebrata. He divides the "Stamm" into three subgroups Tetrapoda, Pisces and Tunicata, and makes no allowance for amphioxus. He proposes two new classes of "Tetrapoda," Hemispondyla and Microsauria with the ordinary classes Amphibia, Reptilia, Aves and Mammalia. The forms he groups in his new class Hemispondyla are the branchiosaurs and a new group which he calls Sclerocepholi. Dr. Jaekel has made several bad blunders in this classification. The first one is to separate the branchiosaurs from the Amphibia, to which they belong without the slightest shadow of a doubt. The next one is the alliance of *Amphibamus* to the Branchiosauridæ, to which it is not so closely allied as it is to the Cotylosauria. *Amphibamus* is far removed in structure from the Branchiosauridæ. His next error is the inclusion of *Acanthostoma* in the same group with the Branchiosauridæ. Their structures do not indicate relationships at all.

His class Microsauria is wholly untenable, as Dr. Williston well says (17). The group which we call Microsauria now will undoubtedly require revision and it looks as if it were going to get

it, but that the animals now included in that group represent a class distinct from all other vertebrates I, for one, will not for a moment concede.

The fundamental error made by Dr. Jaekel, as the reviewer sees it, is the attempt to base a classification of vertebrates on a single character. This has always failed in the the past and must, in the nature of the case, fail in the future; since classification, if it is to mean anything, must take into consideration the entire organization. The paper is full of many other smaller errors, errors of knowledge and errors of judgment. One of these errors is relating such widely distinct forms as *Ceraterpeton* and *Diplocaulus*.

The same author has given a study of the limbs of the oldest vertebrates in which (15) he attempts to sustain his classification, but his facts and arguments are not at all convincing and the paper is little more than a republication of parts of the essays of other investigators.

Dr. Williston (17) has recently published another essay on the Permian fauna of Texas in which he gives especially a study of the vertebræ and adopts the view of Cope as to the ultimate fate of the elements of the rhachitomous vertebra. He regards *Eosauravus copei* Will. (*Eosauravus punctulatus* (Cope)) as allied to *Hylonomus* and for that reason "the oldest known reptile" is a microsaur. Just what his reasons for this alliance are he does not say. In the present imperfect state of our knowledge of *Hylonomus* and its Canadian brothers such a reference would be very uncertain. In the last paragraph he records the interesting discovery of limbs in *Lysorophus*.

A general review of the above essays shows that more than half of them represent pioneer work, that is, descriptive and classificatory investigations. Five of the essays bear more largely on the faunal relations as exhibited by the Amphibia. One gives us new light on the significance of a structure found in the ancient forms. This is where work is greatly needed. Our knowledge of the ancient amphibian fauna will increase as time goes on but the greater part of the pioneer work is already done. The way is now open for some good investigations on the structure of the ancient Amphibia and the meaning of these characters as interpreted in the light of modern comparative anatomy and embryology.

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ROY L. MOODIE.

UNIVERSITY OF KANSAS.